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Early Tertiary Vertebrate Faunas, Trans-Pecos Texas: Ceratomorpha Less Amynodontidae

John Andrew Wilson
and
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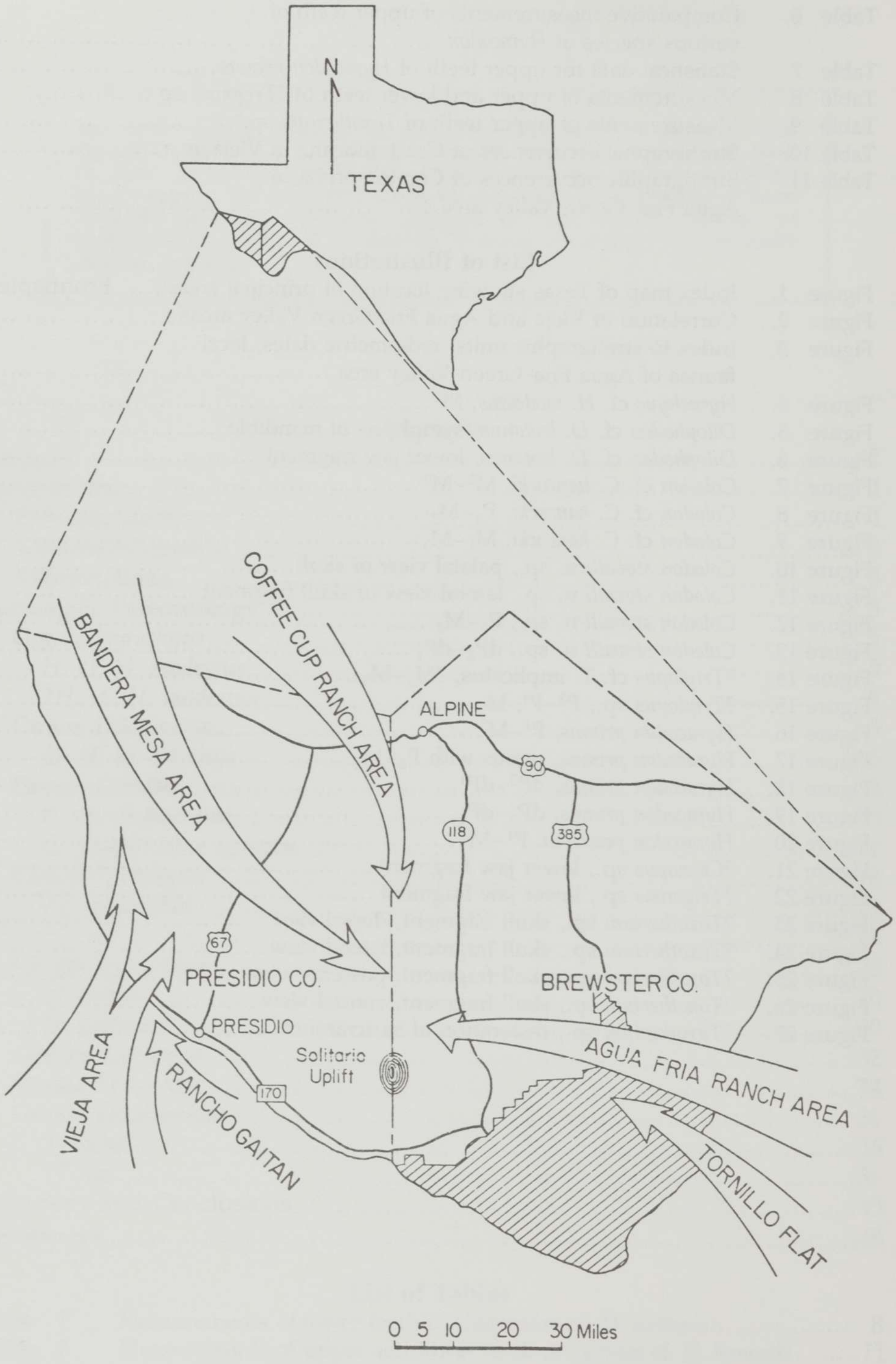

Fig. 1.—Map of Texas with Presidio and Brewster Counties shaded. Enlarged map shows location of principal fossiliferous areas. Shaded area of enlarged section is Big Bend National Park.

EARLY TERTIARY VERTEBRATE FAUNAS, TRANS-PECOS TEXAS: CERATOMORPHA LESS AMYNODONTIDAE

John Andrew Wilson[1]
and
Judith A. Schiebout[2]

ABSTRACT

Ceratomorph remains found in Eocene and Oligocene deposits of Trans-Pecos Texas are herein described, except for the amynodonts which were described in a previous paper. *Hyracodon primus, Hyracodon petersoni,* and *Colodon stovalli* n. sp. are described from well-preserved material; *Hyrachyus* and *Dilophodon* are not so well represented. *Triplopus, Caenopus,* and *Trigonias* are questionably identified and a skull fragment is provisionally referred to *Toxotherium.*

Changes in faunal lists of Trans-Pecos local faunas are reported.

Generalized stratigraphic sections of the Vieja and Agua Fria-Green Valley areas are provided.

INTRODUCTION

Ceratomorph remains have been found in upper Eocene and lower Oligocene deposits of the Vieja area and the Agua Fria, Green Valley, and Coffee Cup Ranch areas (fig. 1) in Trans-Pecos Texas. We have already described the amynodonts (Wilson and Schiebout, 1981), and earlier papers by Schiebout (1977) and Harris (1967) described, respectively, *Schizotheroides* and *Toxotherium*. Generalized stratigraphic sections are given for both areas (figs. 2, 3). *Hyracodon primus, H. petersoni,* and *Colodon stovalli* n. sp., are the taxa represented by the best-preserved material; *Hyrachyus* and *Dilophodon* are less well represented. *Triplopus, Caenopus,* and *Trigonias* are questionably identified. The posterior part of a skull is questionably referred to *Toxotherium.*

PREVIOUS WORK

This is one of a series of papers that deal primarily with the fossil vertebrate faunas of Trans-Pecos Texas. Previous papers in the series are: McGrew (1953), Wilson (1966), Hoffer and Wilson (1967), Harris (1967), Wilson *et al.* (1968), Forsten (1971a,b), Harris and Wood (1969), Wilson (1971a,b), Wood (1973,1974), Schiebout (1974), Wilson (1974), Novacek (1976), Wilson and Szalay (1976), Szalay and Wilson (1976), Schiebout (1981), and West (1982). This publication is a contribution of the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

Wilson and Schiebout (1981) described a large collection of *Amynodon advenus* from the Whistler Squat local fauna and a smaller collection of amynodont remains from higher in the stratigraphic section in the Green Valley area and from the Vieja area.

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N.A. LAND MAMMAL AGE		VIEJA-OJINAGA AREA: Lithologic unit	VIEJA-OJINAGA AREA: K/Ar	VIEJA-OJINAGA AREA: Local fauna Mexico	VIEJA-OJINAGA AREA: Local fauna Texas	AGUA FRIA-GREEN VALLEY AREA: Lithologic unit		AGUA FRIA-GREEN VALLEY AREA: K/Ar	AGUA FRIA-GREEN VALLEY AREA: Local fauna or locality
CHADRONIAN		Mitchell Mesa Rhyolite	32.28		Ash Spring (Vieja Group undif.) Airstrip	Mitchell Mesa Rhyolite		32.28	
								33.04 basalt	
		Capote Mt. Tuff				Devil's Graveyard Formation: Bandera Mesa Member			Coffee Cup
		Bracks Rhyolite	37.4 37.7	Rancho Gaitan	Little Egypt				
DUCHESNEAN	Late	Chambers Tuff			Porvenir				Montgomery Bonebed
	Early	Buckshot Ignimbrite	37.3 37.0			Middle member	Skyline channels	42.70 tuff	Cotter Channels Skyline
UINTAN	C	Colmena Tuff			Candelaria	Lower member	Titanothere channels		Serendipity
	B							43.90 biotite	
							Basal Tert. congl.	49.70, 46.90 tuff	Whistler Squat

Fig. 2.—Correlation of lithologic units, potassium/argon dates, local faunas, and North American land mammal "ages" from the Vieja-Ojinaga areas to the Agua Fria-Green Valley areas in Trans-Pecos Texas and northern Mexico. K/Ar dates revised according to IUGS (1976). Devil's Graveyard Formation and Bandera Mesa Member are manuscript names from Stevens et al. (1984) and are reserved by the Geologic Names Committee, U.S. Geological Survey.

Remains of other ceratomorphs and tapiroids are less common and also more difficult to treat taxonomically. Those considerations influenced our decision to delay publication of the description in the hope of obtaining more and better material. Some new material, mostly from the Green Valley area, has helped to supplement that obtained earlier from the Vieja area. This publication covers the last major taxonomic group from the local faunas of the Vieja area. Some changes need to be made in the faunal lists of local faunas given in Wilson (1977). They are mentioned at the appropriate place in this publication.

The manuscript names Devil's Graveyard Formation and Bandera Mesa Member (fig. 3) have been proposed by J. B. and M. S. Stevens and J. A. Wilson (1984) and have been reserved by the Committee on Geologic Names of the United States Geological Survey. The name Pruett Formation is used in the text of the present paper but is abandoned in the other manuscript because the top of the Pruett Formation was defined by Goldich and Elms (1949) as the base of the Crossen Trachyte and the Crossen Trachyte does not extend as far south as the Agua Fria area.

Length and width measurements of the upper cheek teeth given in this paper are the greatest length along the ectoloph and the greatest width along the protoloph. Lower teeth were measured along the greatest length and width. All measurements are in millimeters.

The crown-height index, as used by Radinsky (1967b), is the paracone height of the unworn M^3 divided by its width. We have used the same measurement for *Hyracodon*.

Detailed descriptions of localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

ABBREVIATIONS

@	measurement approximate
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania
CM	Carnegie Museum, Pittsburgh, Pennsylvania
CMNH	Colorado Museum of Natural History, Denver, Colorado
est	estimate
FMNH	Field Museum of Natural History, Chicago, Illinois
L	anteroposterior length
l.f.	local fauna
M	mean
m	(in text) meters
m	(in tables) minimum
m.y.	millions of years before present
N	number
NMC	National Museum of Canada, Ottawa
OR	observed range
OU	University of Oklahoma, Norman, Oklahoma
PRC	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
TMM	Texas Memorial Museum, The University of Texas at Austin
UOMNH	University of Oregon Museum of Natural History, Eugene, Oregon
USNM	United States National Museum, Washington, D.C.
W	width
YPM	Yale Peabody Museum, New Haven, Connecticut

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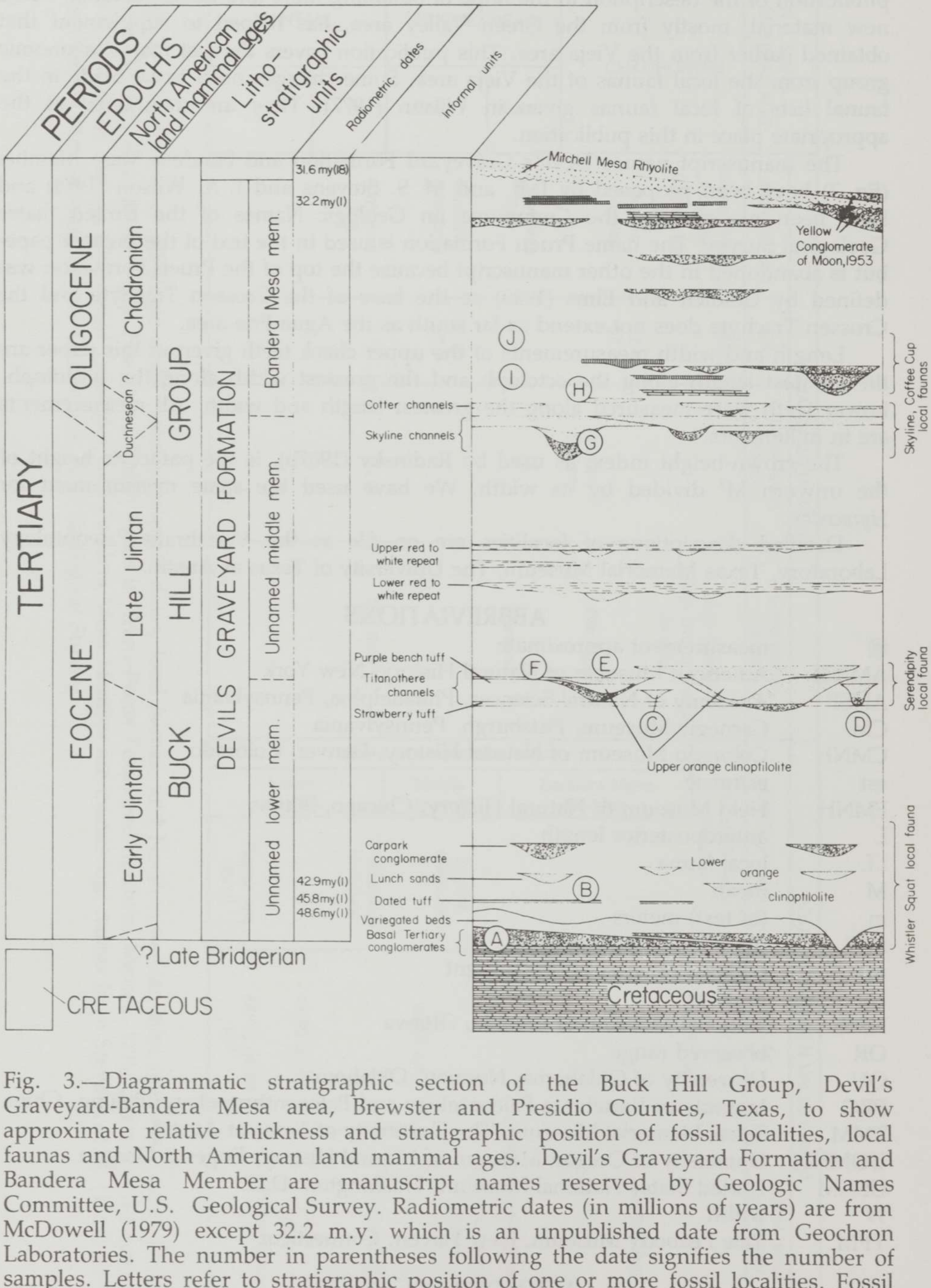

Fig. 3.—Diagrammatic stratigraphic section of the Buck Hill Group, Devil's Graveyard-Bandera Mesa area, Brewster and Presidio Counties, Texas, to show approximate relative thickness and stratigraphic position of fossil localities, local faunas and North American land mammal ages. Devil's Graveyard Formation and Bandera Mesa Member are manuscript names reserved by Geologic Names Committee, U.S. Geological Survey. Radiometric dates (in millions of years) are from McDowell (1979) except 32.2 m.y. which is an unpublished date from Geochron Laboratories. The number in parentheses following the date signifies the number of samples. Letters refer to stratigraphic position of one or more fossil localities. Fossil localities referred to in this paper are: A. 41443, Junction; C. 41672, Purple Bench; H. 41929, upper Red Table silts, Cotter Ranch; J. Base of McKinney Mt. Stratigraphic section compiled by James B. and Margaret S. Stevens, Lamar University, Beaumont, Texas.

Texas at Austin, have supported the field work, the laboratory preparation, and, in part, the cost of publication.

We are especially grateful to Dr. William D. Turnbull and Dr. Rainer Zangerl of the Field Museum of Natural History, Chicago, for the loan of material and for information and photographs concerning ceratomorph material in their collection. We acknowledge and thank for courtesies Dr. Mary Dawson, Dr. R. J. Emry, Dr. L. B. Radinsky, and Dr. D. E. Savage. Dr. James B. Stevens and Margaret S. Stevens worked out the stratigraphic sequence in the Agua Fria area. Mr. and Mrs. Billy Pat McKinney, the lessees, and Messrs. H. J. Burton, Sid Burton, and Macon Richmond, owners of the Agua Fria Ranch, provided invaluable assistance to field parties. The upper reaches of the Alamo de Cesario extend onto the ranch of Dr. Walter W. Dalquest of Midwestern University, who generously permitted access to his land. Mr. and Mrs. Clegg Fowlkes of Marfa, Texas, have been most helpful in giving us access to their ranches in the Green Valley area.

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SYSTEMATIC PALEONTOLOGY

Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Superfamily Tapiroidea Gill, 1872
Family Helaletidae Osborn, 1892
Subfamily Hyrachyinae Osborn, 1892, sensu Radinsky (1967a)
Genus *Hyrachyus* (Leidy) 1870

Radinsky (1966, 1967a) proposed that *Hyrachyus* be placed in the superfamily Tapiroidea rather than in the Rhinocerotoidea where it had resided for many years. This proposal (Radinsky, 1966, p. 632) was based on the following dental characters: "primitive ceratomorph [dentition] with large parastyles, unmodified molar metacones and low metalophids and paralophids." In his 1967a paper he wrote: "*Hyrachyus* appears to have given rise to the early Uintan hyracodontid rhinocerotoid *Triplopus* through the late Bridgerian *Hyrachyus modestus*." On the other hand, Tanner and Martin (1972) stated: "The Hyrachyinae probably gave rise to the hyracodontids independently from the Rhinocerotoidea and if the Hyrachyinae is included within the tapirs, so should the hyracodontids which are tapir-like in the presence of dP^1, as well as in the form of their canines and incisors, be included in the Tapiroidea."

The material from Texas is not sufficiently complete to offer a solution to the dilemma. However, it is questionable that all members of the superfamily Tapiroidea had a replaced dP^1. In *Colodon*, for example, a replaced dP^1 is not known (Radinsky, 1963, p. 60), yet *Colodon* is placed in the Tapiroidea. A replaced dP^1 is also not known in *Amynodon advenus* (Wilson and Schiebout, 1981), yet *Amynodon advenus* is placed in the superfamily Rhinocerotoidea. The presence or absence of dP^1 is not consistent at a superfamily level so we prefer to follow Radinsky (1966, 1967a) and place *Hyrachyus* with the tapirs.

Hyrachyus cf. *H. modestus*
Figure 121 in Wilson (1967)

Referred material.—TMM 40145-1, M^1 or M^2

Stratigraphic position.—Big Yellow Sandstone Member, Canoe Formation, Big Bend National Park, Texas.

Age.—?Bridgerian age

Description.—An M^1 or M^2 of *Hyrachyus* sp. (TMM 40145-1) was briefly described by Wilson (1967, p. 169, fig. 121). It has the large paracone and unmodified metacone

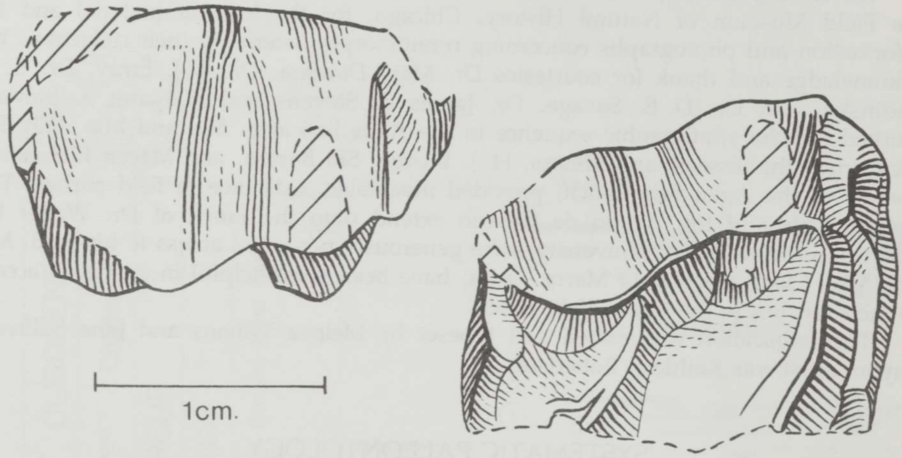

Fig. 4.—?*Hyrachyus* cf. *modestus*, TMM 41443-626. M^2 fragment. External and occlusal views. Whistler Squat local fauna, Pruett Formation.

of *Hyrachyus* and falls within the observed range of either M^1 or M^2 of *H. modestus*. Nothing more can be added to the paleontologic description of this taxon until more material has been recovered.

?*Hyrachyus* cf. *H. modestus*
Whistler Squat local fauna
Figure 4

Referred material.—TMM 41443-626, M^2.

Stratigraphic position.—Basal Tertiary conglomerate, Agua Fria Quadrangle, Brewster Co., Texas.

Age.—Early Uintan, Wagonhound. Whistler Squat local fauna.

Description.—A large tapiroid in the Whistler Squat local fauna is represented by the external two-thirds of an M^2 (TMM 41443-626; fig. 4). The parastyle is broad, rounded, and typically tapiroid. The buccal surface of the paracone is broken. A prominent crista is present opposite the paracone. The metacone is concave. The bulbous parastyle and the concave metacone are characteristic of *Hyrachyus* and we refer this specimen to ?*Hyrachyus* cf. *H. modestus*. The length of this tooth is 18.0 mm, which is within the observed range of M^2 of *H. modestus*, 14.0–20.2 (N=24) as given by Radinsky (1967a). If our questionable identification should prove to be correct, then the stratigraphic range of *Hyrachyus* would extend to the early Uintan.

Genus *Dilophodon* Scott 1883
Dilophodon leotanus (Peterson), 1931
Dilophodon cf. *leotanus*
Candelaria local fauna
Figures 5, 6; Table 1

Referred material.—TMM 31281-11, lower jaw fragment with symphysis and partial alveoli for C, P_3, P_4, and roots of M_1–M_3.

Stratigraphic position.—In the lower 50 ft (15.2 m) of the Colmena Tuff, about 130 ft (39.6 m) below the Buckshot Ignimbrite.

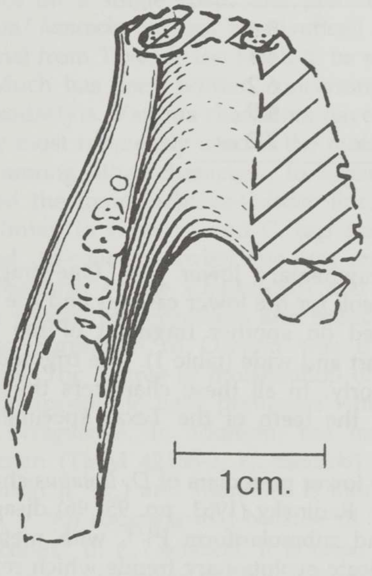

Fig. 5.—*Dilophodon* cf. *leotanus*, TMM 31281-11. Symphysis with alveoli for C, roots of P_2, P_3, and anterior root P_4. Candelaria local fauna, Colmena Tuff.

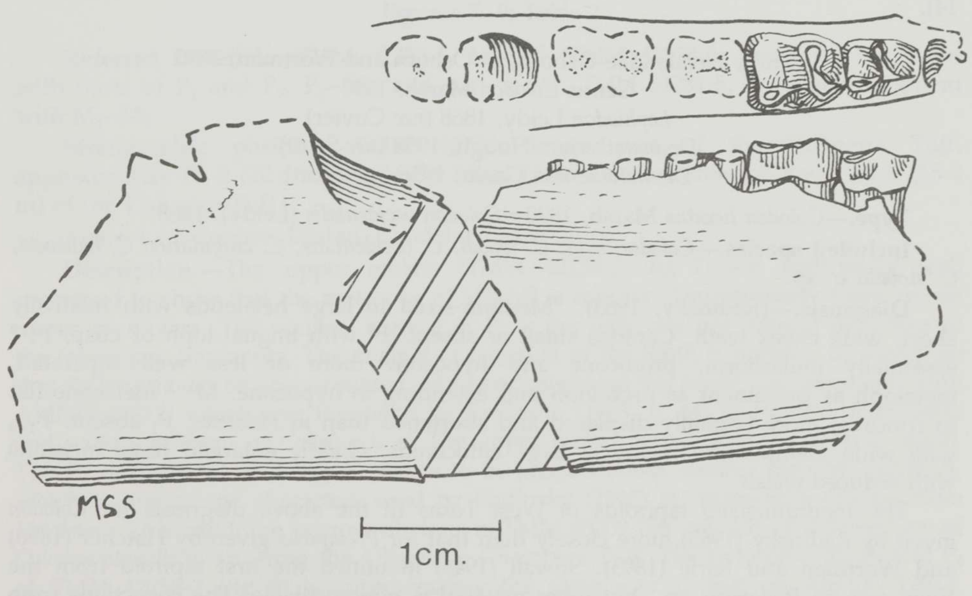

Fig. 6.—*Dilophodon* cf. *leotanus*, TMM 31281-11. Lower jaw fragment, fragment of P_2, P_{3-4}, and roots of M_{1-3}. Candelaria local fauna, Colmena Tuff.

Table 1.—Measurements of lower teeth of *Dilophodon* cf. *leotanus* from Texas.

		TMM 31281-11
P_3	L	5.6
	W	4.1
P_4	L	6.2
	W	4.9
M_1	L	7.2 est

Age.— Late Eocene, Myton Uintan.

Description.—The only specimen is a fragmentary lower jaw. One fragment shows the innermost section of rather large alveoli for the lower canines and the roots of P_2 and P_3 (fig. 5). P_3 and P_4 are preserved on another fragment of the same specimen (fig. 6). Both of the premolars are short and wide (table 1). The trigonids are rounded and the talonids are basined posteriorly. In all these characters the Texas specimen closely resembles *Colodon,* although the teeth of the Texas specimen are much smaller.

Discussion.— Gazin (1956) thought that the lower premolars of *D. leotanus* showed characters that seemed to relate it to *Protapirus*. Radinsky (1963, pp. 95–96) disagreed and said that "Small size, shortened P_{2-4}, and submolariform P^{2-4}, with metaloph bypassing hypocone, in *Dilophodon leotanus* indicate evolutionary trends which remove the *Dilophodon* lineage from tapirid origins." The Texas specimen has the foreshortened P_3–P_4. It also has a short symphysis and in this character is more similar to *D. leotanus*. The above characters, few though they are, tend to support the views of Radinsky (1963) that *Dilophodon* is a small helaletid that evolved in a line parallel to that of *Helaletes-Colodon*.

This specimen was listed as "*Dilophodon* n. sp." in Wilson (1977b, Tables 1,2, and 14).

Family Helaletidae Osborn, in Osborn and Wortman, 1892
Genus *Colodon* Marsh, 1890
Lophiodon Leidy, 1868 (*nec* Cuvier)
Desmatotherium Hough, 1955 (*nec* Scott)
Desmatotherium Gazin, 1956 (*nec* Scott)

Type.— *Colodon luxatus* Marsh, 1890 = *Colodon occidentalis* (Leidy), 1868.

Included species.— *Colodon kayi, C. woodi, C. occidentalis, C. cingulatus, C. hancocki, C. stovalli* n. sp.

Diagnosis.— (Radinsky, 1963). "Medium-sized to large helaletids with relatively short, wide cheek teeth. Canines small or absent. P^1 with lingual loph or cusp; P^{2-4} essentially molariform, protocone and hypocone more or less well separated, metaloph as prominent as protoloph and extending to hypocone. M^{1-2} metacone flat to concave, more lingually displaced and shortened than in *Helaletes*. P_1 absent. P_{2-4} with wide talonids and relatively large entoconids. Greatly enlarged nasal incisions with reduced nasals."

The medium-sized tapiroids of West Texas fit the above diagnosis for *Colodon* given by Radinsky (1963) more closely than that for *Protapirus* given by Hatcher (1896) and Wortman and Earle (1893). Stovall (1948) identified the first tapiroid from the Vieja area as *Protapirus* sp., but more material is now available. The collections from the University of Oklahoma, the Field Museum of Natural History, and The University of Texas at Austin are included herein. Our reasons for assigning all of the

material to *Colodon* rather than *Protapirus* are the following: P_2 is short; M_3 has a strong hypoconulid. The lower canine is present but is very small. Two internal cusps are distinguishable on P^2 (N=4) and P^3 (N=3) but they are very close together. On P^4 (N=3) two have only a single cusp but with an internal groove and one has two wear facettes on a single cusp. The premolars are slightly more advanced than those of *Colodon*? *hancocki* but not as advanced as those of *C.*? *cingulatus* or *C. occidentalis*. The material from Texas is too small to be referred to *Protapirus*.

Much has been written concerning the occlusal pattern of the teeth of the early perissodactyls. Various characters have been emphasized by different authors, but one of the most frequently used is the molarization of the premolars. Radinsky (1963) used this, among other characters, to separate two lineages of *Colodon*. In one, which he termed the main *Helaletes-Colodon* line, the premolars became molariform as early as the Uintan in *C. woodi* and *C. kayi* and more so in the Oligocene *C. occidentalis*. The second, so-called retarded line was only questionably referred to *Colodon* because his *C.*? *cingulatus* of the Chadronian and Orellan have nonmolariform premolars and a lesser degree of depression and reduction of the metacone. His *C.*? *hancocki* from the Clarno Formation of Oregon was questionably referred to *Colodon* for the same reasons. The degree of molarization of premolars is difficult to measure but the Texas sample appears to have premolars which are less molariform than either *C. occidentalis* or *C.*? *cingulatus*. In addition, the metacone of M^2 is convex on both the Eocene specimen (TMM 42158-2, *C. hancocki*) and the Oligocene specimen (FMNH PM 104, *C. stovalli* n. sp.) and therefore is more similar to Radinsky's retarded line. Radinsky (1963, p. 96) suggests that because of "the nonmolariform premolars and convex M^{1-3} metacones" in *C.*? *hancocki*, it is close to the origin of the tapirid line. However, the short and wide lower premolars in the Texas specimens are closer to *Colodon* than to *Protapirus*. Therefore we elect to include *C. cingulatus* and *C. hancocki* in the genus *Colodon* without query and to propose a new species, *C. stovalli*, for the conservative tapiroids from the early Chadronian Porvenir and Little Egypt local faunas.

Colodon cf. *hancocki* Radinsky 1963
Candelaria local fauna
Figures 7–9; Table 2

Referred material.—TMM 42258-2, M^1–M^3. TMM 42258-3, lower jaw fragment with parts of P_2 and P_3, P_4–M_2, and part of M_3. TMM 31281-5, lower jaw fragment with M_1–M_3.

Stratigraphic position.—TMM 42258, lower part of the Colmena Tuff, approximately 75 ft (22.8 m) above the base; TMM 31281, within the lower 50 ft (15.2 m) of the Colmena Tuff.

Age.—Late Eocene, Uintan. Candelaria local fauna.

Description.—The upper molars (TMM 42258-2, fig. 7) are sufficiently well preserved to show that the metacone of M^2–M^3 is concave. Unfortunately there are no upper premolars. The occlusal surface of P_2 is the only one not present on either of the lower jaw fragments. The enamel of one side of the tooth is present, however, so that its length can be approximated. We have compared the lower jaw specimens with AMNH 12672, which was identified by Radinsky (1963, p. 44) as *Helaletes intermedius* and with specimens of *Colodon kayi*. The upper molars were compared with *C. woodi*. The P_4 of TMM 42258-3 (fig. 8) seems to be proportionally shorter than M_1 (table 2), which is one of the characters used by Radinsky (1963) to distinguish *Colodon* from *Helaletes*. This condition is more obvious in TMM 40209-759 (fig. 13)—the lower jaw of *Colodon stovalli* n. sp. from the Oligocene Chambers Tuff. The entoconid on P_3 and P_4 of TMM 42258-3 (fig. 8) is approximately the same size as that on AMNH 12672, although those teeth are more worn in the Texas specimen. The entoconid on the P_4 of TMM 40209-759 from the Chambers Tuff is large. This is also a character used by

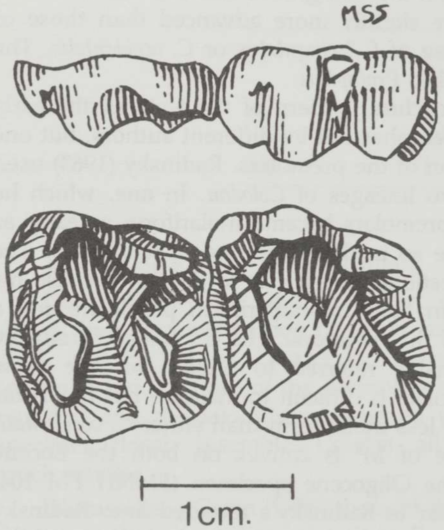

Fig. 7.—*Colodon* cf. *hancocki*, TMM 42258-2. M^{2-3}. Candelaria local fauna, Colmena Tuff.

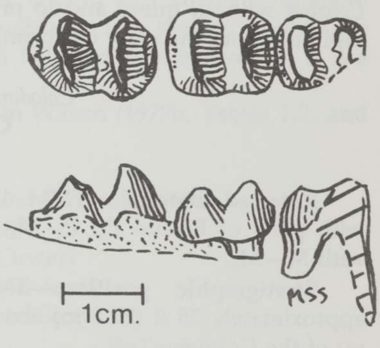

Fig. 9.—*Colodon* cf. *hancocki*, TMM 31281-5. M_{1-3}. Candelaria local fauna, Colmena Tuff.

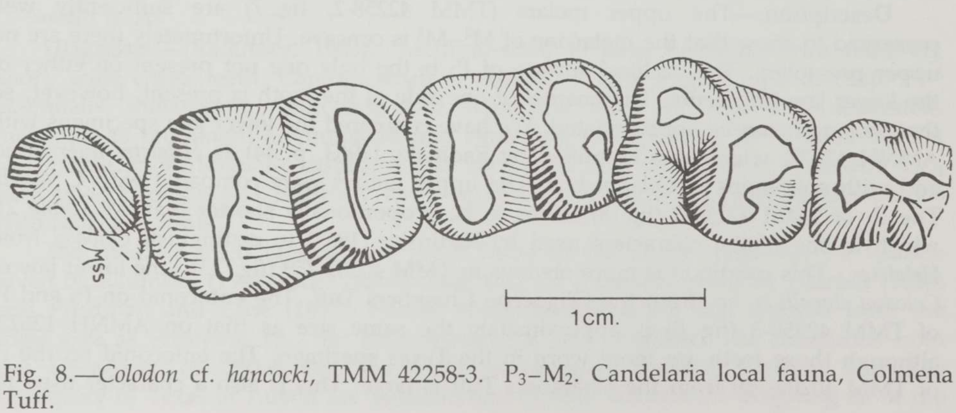

Fig. 8.—*Colodon* cf. *hancocki*, TMM 42258-3. P_3–M_2. Candelaria local fauna, Colmena Tuff.

Table 2.—Measurements of upper and lower teeth of *Colodon* cf. *hancocki* from Texas.

Upper Teeth		TMM 42258-2	Lower Teeth		TMM 42258-3	TMM 31281-5
M^1	L	12.0	P_2–P_4		27.6	—
	W	14.3	M_1–M_3		42. est	—
M^2	L	14.5	P_2	L	8.8	—
	W	15.1		W	—	—
M^3	L	14.3	P_3	L	9.5	—
	W	15.7		W	—	—
			P_4	L	9.8	—
				W	7.1	—
			M_1	L	11.4	12.0
				W	7.2	9.1
			M_2	L	13.2	13.5
				W	9.3	10.3
			M_3	L	—	11.6
				W	—	10.9

Radinsky (1963) to separate *Helaletes* from *Colodon*. TMM 31281-5 (fig. 9) from the Colmena Tuff has the M_3 preserved. This tooth has a very small hypoconulid and in this character is like AMNH 12672 (*H. intermedius*) and UOMNH 20376 (*C. hancocki*). All five of the M_3s of *C. stovalli* n. sp. have very well-developed hypoconulids.

Discussion.—The late Eocene tapiroids are poorly known, and this material from Texas only extends the geographic range of the taxonomic confusion. The lower jaw material could be assigned to *H. intermedius* because of the very small hypoconulid and because the shortening of P_4 relative to M_1 is slight. Such an assignment would extend the stratigraphic range of *H. intermedius* from Bridgerian to late Uintan. On the other hand, the Texas specimens lie between *Colodon woodi* and *C. kayi* in size. The samples of these two species are from the late Uintan of Montana and Wyoming and are also small. Radinsky (1963, p. 59) stated that "M_3 hypoconulid varies greatly in length and width and is unreliable as a taxonomic criterion." However, Bruce Hanson (personal communication, 1973) compared the Texas material from the Colmena Tuff to *Colodon*? *hancocki* Radinsky from the Hancock Quarry, Clarno Formation of Oregon and said that they are "virtually indistinguishable." We therefore believe that it is best to refer the late Eocene material from the Colmena Tuff to *Colodon* cf. *hancocki* pending the discovery of more and better material.

Colodon stovalli n. sp.
Porvenir and Little Egypt local faunas
Figures 10–13; Table 3

Type.—FMNH PM 104, skull fragment with left P^2–M^3, right P^3, fragment M^2, M^3.

Etymology.—Named for the late Professor J. Willis Stovall of the University of Oklahoma, a pioneer collector of fossil vertebrates in the Vieja area of West Texas.

Referred material.—Right maxilla consisting of OU 17-2-52a plus TMM 40206-37, the former with internal halves of P^3–P^4 and M^2, and the latter with fragment of P^1 and internal half of P^2. OU 17-2-52b, left maxilla of same individual with internal half of P^3. FMNH PM 30, skull fragment with M^2. FMNH PM 127, skull fragment with M^3. TMM 40688-37, fragmentary P^1 and P^2, internal half of P^3. TMM 40845-2, P^2. FMNH

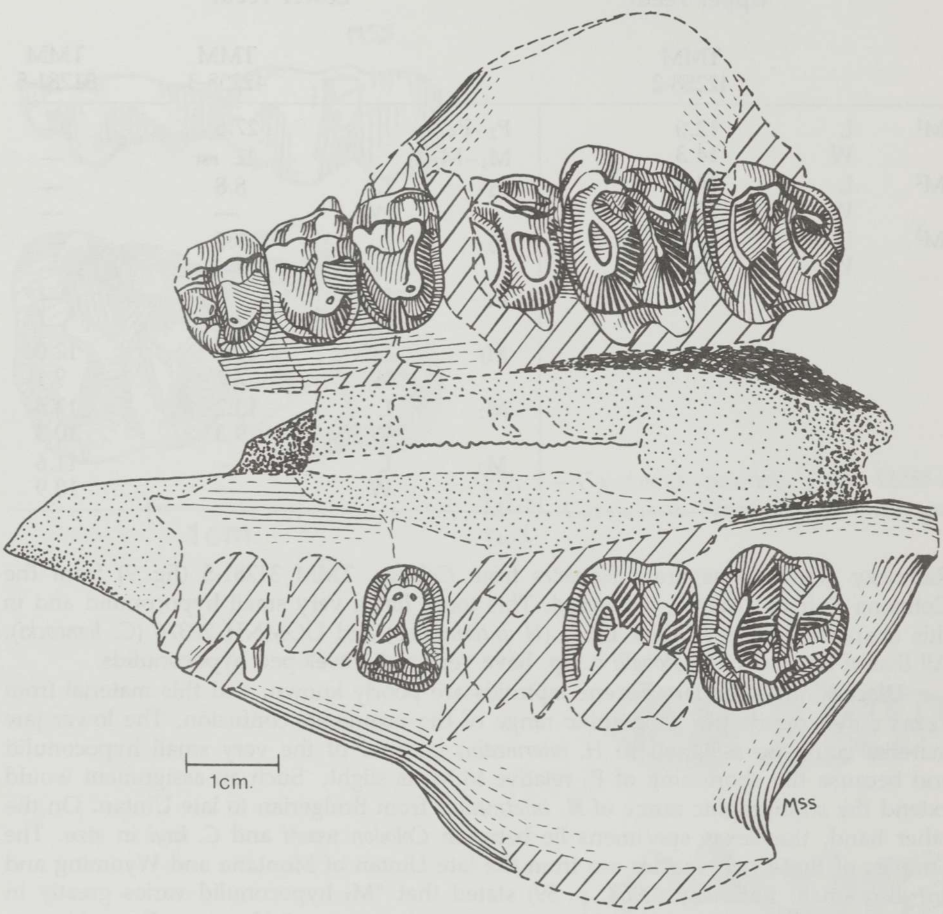

Fig. 10.—*Colodon stovalli* new species, type, FMNH PM 104. Skull fragment with left P^2–M^3. Porvenir local fauna, Chambers Tuff.

PM 59, M^1. TMM 40688-10, fragmentary dP^4, M^1–M^2. TMM 40492-23, dP^4. TMM 40209-759, lower jaw with alveolus for right I_1–I_3 and C, P_2–P_3, fragment P_4, M_1–M_3; left alveolus for I_1, P_4 and fragment M_3. FMNH PM 147, lower jaw fragment with posterior half M_1, M_2. FMNH PM 148, lower jaw fragment with P_4, M_2. FMNH PM 78, lower jaw fragment with M_3. FMNH PM 77, lower jaw fragment with anterior part of M_3. TMM 40731-1, lower jaw fragment with M_1–M_2. TMM 40206-34, lower jaw fragment with P_4, M_2. TMM 40688-44, lower jaw fragment with P_2, P_3. TMM 40688-81, lower jaw fragment with M_2. TMM 40492-12, lower jaw fragment with dP_2–dP_4, unerupted M_1.

Stratigraphic position.—Chambers Tuff below and above the lower marker bed in the "Big Red Horizon" and "Blue Cliff Horizon" of the field notes of Bryan Patterson in the Field Museum of Natural History (Wilson, 1977b, fig. 7). TMM 40492, red mound north of Big Cliff, less than 5 ft [1.3 m] below the lower marker bed in the Chambers Tuff (Wilson, 1977b, table 5). The stratigraphic position of the collection of

Table 3.—Measurements of upper and lower teeth of *Colodon stovalli* n. sp. from Texas.

Upper Teeth

		FMNH PM 104	FMNH PM 30	FMNH PM 127	OU 17-2-52a	TMM 40688-10	FMNH PM 59	TMM 40845-2
P^1–M^3		—	—	—	85. est	Juv.	—	—
P^1–P^4		—	—	—	42. est	—	—	—
M^1–M^3		43. @	—	—	45. est	—	—	—
P^1	L	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—
P^2	L	10.0 @	—	—	—	—	—	10.2
	W	14.2	—	—	—	—	—	13.4
P^3	L	9.8	—	—	—	—	—	—
	W	14.6	—	—	—	—	—	—
P^4	L	10.6	—	—	—	—	—	—
	W	15.5	—	—	—	—	—	—
M^1	L	—	—	—	—	13.7	13.6	—
	W	—	—	—	—	16.5	16.2	—
M^2	L	15.6	14.2	—	15.8	—	—	—
	W	18.6	16.6	—	18.4	—	—	—
M^3	L	15.7	—	16.0	—	—	—	—
	W	17.4	—	19.2	—	—	—	—

Lower Teeth

		TMM 40209-759	TMM 40688-44	TMM 40206-34	TMM 40731-1	FMNH PM 147	FMNH PM 77	FMNH PM 19	FMNH PM 57	OU 17-4-52	TMM 40492-12
P_2	L	9.1	—	—	—	—	—	—	—	—	—
	W	7.3	7.8	—	—	—	—	—	—	—	—
P_3	L	9.5	11.0	—	—	—	—	—	—	—	—
	W	8.7	10.8	—	—	—	—	—	—	—	—
P_4	L	—	—	12.7	—	—	—	—	10.7	—	—
	W	10.0	—	11.2	—	—	—	—	11.2	—	—
M_1	L	12.4	—	—	13.2	—	—	—	—	—	—
	W	8.7	—	—	9.4	9.5	—	—	—	—	—
M_2	L	13.3	—	16.4	14.4	15.2	—	—	—	15.4	—
	W	9.9	—	12.0	11.1	11.3	—	—	—	10.9	—
M_3	L	19.8	—	—	—	—	—	21.5	22.0	—	—
	W	10.7	—	—	—	—	12.3	10.9	13.1	12.5	—
dP_2	L	—	—	—	—	—	—	—	—	—	11.0
	W	—	—	—	—	—	—	—	—	—	6.8
dP_3	L	—	—	—	—	—	—	—	—	—	11.9
	W	—	—	—	—	—	—	—	—	—	7.5
dP_4	L	—	—	—	—	—	—	—	—	—	12.3
	W	—	—	—	—	—	—	—	—	—	13.2

the University of Oklahoma was uncertain because the geographic position of the locality as given by Stovall (1948, map) would have meant that the Oklahoma collection had come from the Colmena Tuff below the Buckshot Ignimbrite rather than from the Chambers Tuff which overlies the Buckshot. However, the Oklahoma collection is obviously from the Chambers Tuff and Wilson (Wilson et al., 1968, p. 597) expressed the suspicion that the O.U. locality had been misplaced on the map. By good luck, OU 17-2-52a, a fragment of the anterior part of the right maxillary, fits against TMM 40206-37. The latter was collected just north of Big Cliff from the lower part of the Chambers Tuff, thus confirming the stratigraphic position of the University of Oklahoma collection. The well-preserved lower jaw, TMM 40209-759, was found at Reeves Bonebed which is approximately 60 ft below the top of the Chambers Tuff (Wilson, 1977, fig. 9).

Age.—Early Chadronian.

Diagnosis.—Smaller than the size for the sample given by Radinsky (1963, table 11) for *C.? cingulatus* and approximately the same size as *C.? hancocki* (Radinsky, 1963, table 12, fig. 13); however, the Montana, Oregon, and Texas samples are small. Lingual cusps on P^2–P^3 barely distinguishable. Internal cusp on P^4 single but with lingual groove. Metacones are strongly depressed lingually. Lower canine vestigial, upper canine unknown. Nasal incision extends to P^4. Large hypoconulid present on M_3.

Description.—The upper dentition is best preserved in FMNH PM 104 (fig. 10), but P^1 is missing from both sides of this specimen. TMM 40206-37 has the posterointernal part of P^1 preserved but it can be determined only that the specimen had an elongate cusp and that the tooth was three-rooted. Complete examples of P^2–P^4 are present in FMNH PM 104. The labial portions of these premolars are approximately the same. The parastyle, paracone, and metacone are in line. The paracone is smaller than the metacone on P^2. The posterior loph on P^2 is stronger and extends farther lingually than the anterior loph. TMM 40845-2 is the best preserved of three second premolars that have the lingual half of the tooth. The anterolingual cusp is in the approximate position of a protoconule. It is separated from the more prominent hypocone by a sharp, narrow groove.

The lingual cusp of the left P^3 of FMNH PM 104 is only slightly worn and is a single cusp although an anterolabial extension is separated by a groove marking the incipient separation of the internal cusps. The position of the lingual cusps on P^2 and P^3 of FMNH PM 104 is not side by side as on P^3 of the type of *C. cingulatus* (CM 722) or the P^2 and P^3 of CM 300, which is also *C. cingulatus*. The anterolingual cusp is in a more anterolabial position on P^2 of the Texas specimen, and has the same orientation but is more lingual in position on P^3. On P^2 of TMM 40206-37/OU 17-2-52a (a less worn specimen), the lingual cusps are separated by a groove. The posterior cusp is larger and the anterior cusp is situated more labially. All three examples of the second premolar in the Texas collection are slightly different. The P^2 and P^3 of FMNH PM 104 have a protoloph that is scarcely more than an elongate protoconule. There is a better-developed and more lingually placed and well-separated anterointernal cusp on TMM 40845-2, whereas TMM 40206-37, although more worn, has a less well-separated but still more lingually placed anterointernal cusp. Both specimens of P^4 have a single lingual cusp.

M^2 and M^3 have the metacones strongly deflected lingually, much more so than on M^1. The internal cingulum does not extend internally to the protocones and hypocones on the upper molars. Measurements of upper teeth are given in table 3.

An impression of the nasal bone is preserved on the right side of FMNH PM 104 (fig. 11). If our interpretation is correct, this impression marks the posterior extent of the nasal incision. On the Texas specimen, which is somewhat crushed, the incision reaches as far posterior as the anterior edge of P^4. A matrix-filled groove for the nasal

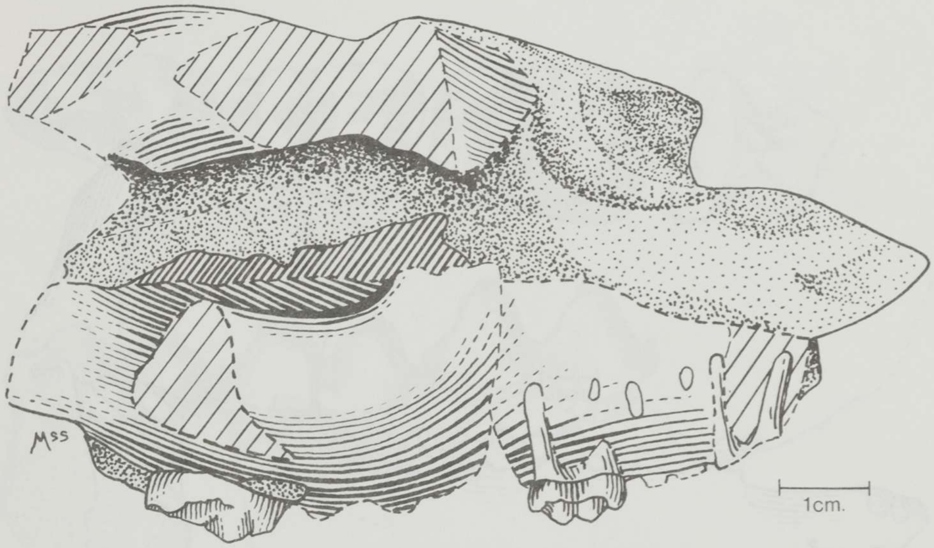

Fig. 11.—*Colodon stovalli* new species, type, FMNH PM 104. Lateral view of right side to show impression of nasal bone that marks edge of nasal incision. Porvenir local fauna, Chambers Tuff.

diverticulum (Radinsky, 1965, p. 78) is present on the upper portion of the ascending process of the maxilla. The nasals are not preserved on FMNH PM 104, so we cannot determine their anterior extent.

The lower dentition is best represented by TMM 40209-759 (fig. 12). Alveoli for the right I_1 and left I_2, I_3, and lower canine are preserved. The roots of I_3 and a lower canine are present, and the latter is a much smaller tooth than the former. A diastema 27.5 mm long separates the root of the lower canine from P_2. The protoconid and hypoconid on P_2–P_4 are connected, and the hypoconid and entoconid are separate. P_2 is triangular, while P_3 is more rounded anteriorly. The entoconids on P_2 and P_3 are smaller than the hypoconids, whereas on P_4 the entoconid and hypoconid are both large cusps which are not connected by a hypolophid. M^3 has a large hypoconulid. Measurements are given in table 3.

The lower milk dentition is present in TMM 40492-12 (fig. 13, table 3). The dP_2 has two lophs and a long paraconid. The paraconid is very similar to, although much smaller than, that on the P_2 of the living Central American tapir. The dP_3 is longer and narrower than dP_4. The hypolophids on dP_2–dP_4 are fully developed and are very different from the hypolophids of their permanent counterparts. An unerupted M_1 is present on TMM 40492-12.

Discussion.—The number of fragmentary specimens of maxillaries or mandibles is considerable, but the total number of any particular tooth is small. Although the diagnostic characters can be determined, little can be learned concerning the range of variation. The Texas sample from the Porvenir local fauna belongs to the group that Radinsky (1963) referred to *"Colodon?"*. He assigned *Colodon cingulatus* Douglas and his new species *C.*? *hancocki* to *"Colodon?,"* giving as his reason (Radinsky, 1963, p. 69):

> However, placing it in *Colodon* would necessitate expansion of the concept of that genus to include a lineage with retarded premolar molarization and perhaps a trend towards increasing molar metacone convexity.

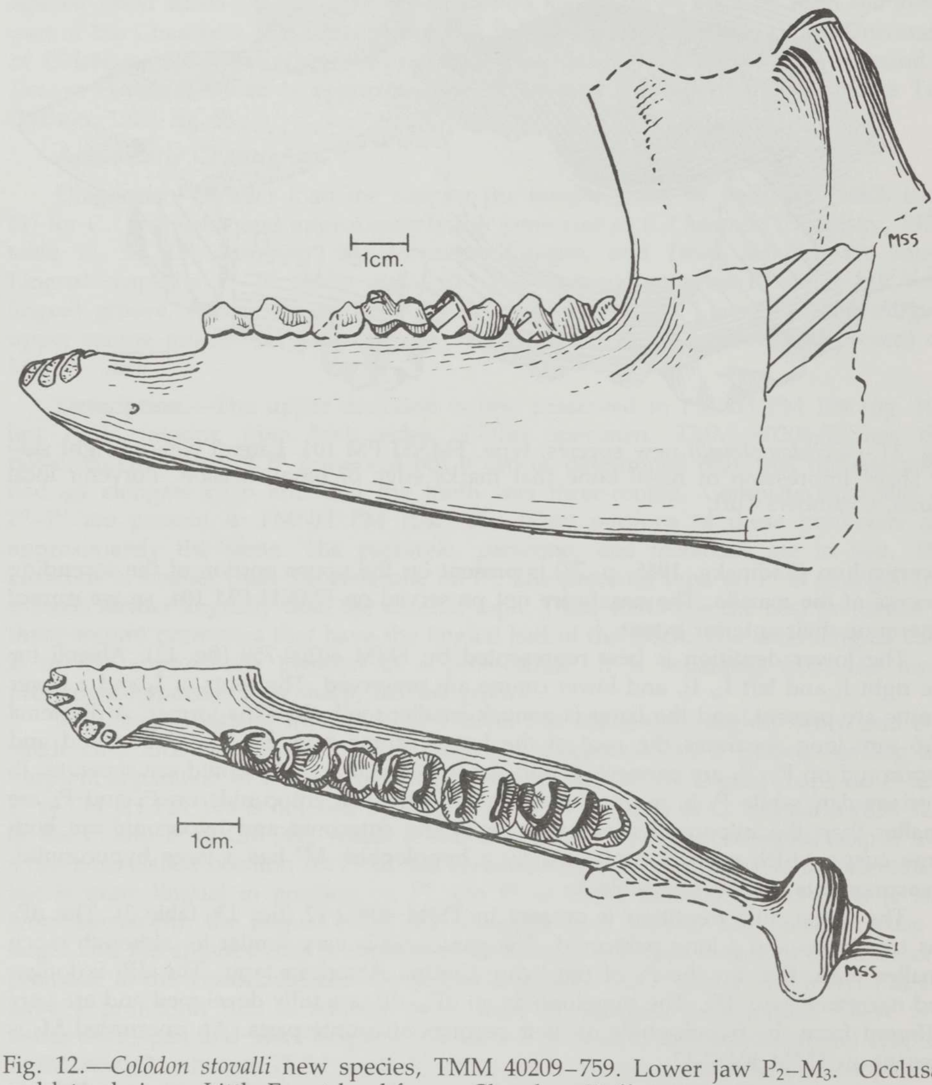

Fig. 12.—*Colodon stovalli* new species, TMM 40209–759. Lower jaw P_2–M_3. Occlusal and lateral views. Little Egypt local fauna, Chambers Tuff.

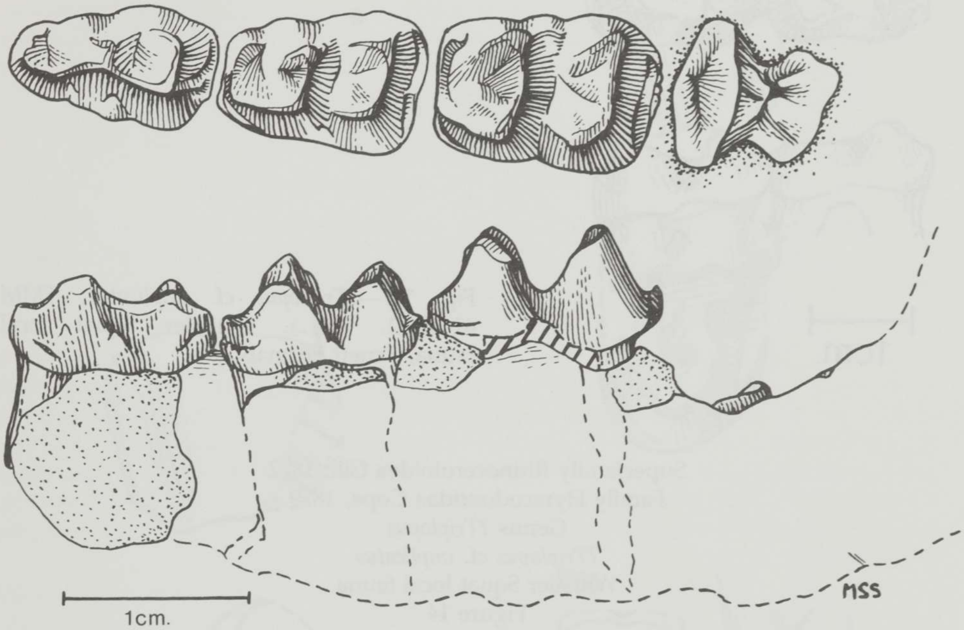

Fig. 13.—*Colodon stovalli* new species, TMM 40492-12. Lower deciduous dentition d P_{2-4} erupting M_1. Porvenir local fauna, Chambers Tuff.

The molarization of the premolars already had been approached by *C. woodi* and *C. kayi* of the late Uintan, and to have the more retarded condition appear later in *C.? hancocki* and *C.? cingulatus* caused Radinsky to question the generic assignment.

A similar situation is found in the molarization of P^4 in the transition from artiodactyl genus *Protoreodon* to *Agriochoerus*. The division of a single labial cusp on P^4 into separate paracones and metacones not only can be shown in all intermediate stages, but can also be shown to have recurred several times (Wilson, 1971a). The tapirs from Texas belong to the more conservative line with *C.? hancocki* and *C.? cingulatus*. In our opinion, *hancocki, cingulatus*, and *stovalli* are most conveniently placed under the "less well separated" protocone and hypocone portion of Radinsky's (1963) definition of *Colodon*. The dental characters of all the late Eocene and very early Oligocene tapiroids are so similar that we agree with Radinsky (1963) that it would be unwise to erect still another genus. The size range of the Texas sample overlaps the small end of the size range of *C. occidentalis*, but what few premolars are available are consistently more conservative. *C. stovalli* n. sp. is close to *C. hancocki*, and we believe that neither is ancestral to *Protapirus* as suggested by Radinsky (1963, fig. 14). The small canine, the short and wide P_2, and the large hypoconulid present in *C. hancocki* and *C. stovalli* are not characteristic of *Protapirus*.

This taxon should be substituted for *Colodon* n. sp. in tables 3, 4, 5, 6, 8, 9, and 14 in Wilson (1977b).

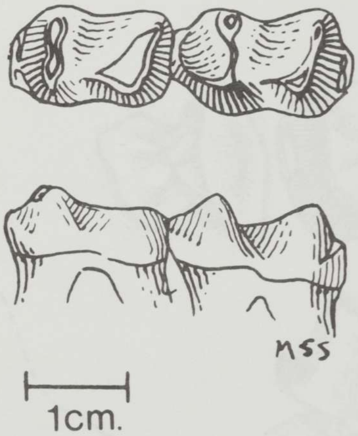

Fig. 14.—?*Triplopus* cf. *implicatus*, TMM 41443–2. ?M_{2-3}. Whistler Squat local fauna, Pruett Formation.

Superfamily Rhinocerotoidea Gill, 1872
Family Hyracodontidae Cope, 1879
Genus ?*Triplopus*
?*Triplopus* cf. *implicatus*
Whistler Squat local fauna
Figure 14

A number of fragmentary jaws and teeth that cannot be referred to species with certainty were found at various levels within the section. They are included here because they indicate the presence of other taxa of ceratomorphs in West Texas.

Referred material.—TMM 41443-2 (fig. 14), lower jaw fragment with ?M_2–M_3. TMM 41443-5 and -6, two isolated P_2s. TMM 41443-3, protoloph and metaloph of M^1.

Stratigraphic position.—Basal Tertiary conglomerate at the "Junction locality".

Discussion.—The dimensions of the teeth of TMM 41443-2 (L 15.5, W 8.5; L 17.3, W 10.0 for M_2 and M_3, respectively) are within the observed range of *Triplopus implicatus* given by Radinsky (1967b, p.13). The dimensions of TMM 41443-5 and -6 (L 10.7, W 6.9; L 10.4, W 6.9, respectively) are slightly above the observed range for P_2 of *Triplopus implicatus* (L 8.0–9.1, W 4.8–5.5), but the sample used by Radinsky was only 2, so that the difference may not be meaningful. TMM 41443-3 is about the same size as the comparable parts of that tooth on AMNH 2341.

Triplopus implicatus retains the metacone on M^3, which is one of the characters Radinsky (1967b) uses to distinguish it from *Epitriplopus uintensis* where the metacone is lost. Both species are medium-sized hyracodonts although *E. uintensis* is slightly larger. Without an upper dentition, we cannot exclude *E. uintensis* with certainty, but the stratigraphic position and the identification of the Whistler Squat local fauna as early Uintan would favor the identification of these specimens as *Triplopus implicatus*.

?*Triplopus* sp.
Serendipity local fauna

Fragmentary specimens of hyracodontids can be identified in the collection from the locality known as Purple Bench. TMM 41672-44, probable M^1, is 13.4 mm long. The lingual half of M^2 and the base of M^3 are preserved on TMM 41672-48. These specimens represent a small hyracodontid probably belonging to the genus *Triplopus*. More material is needed from this locality before certain identification can be made.

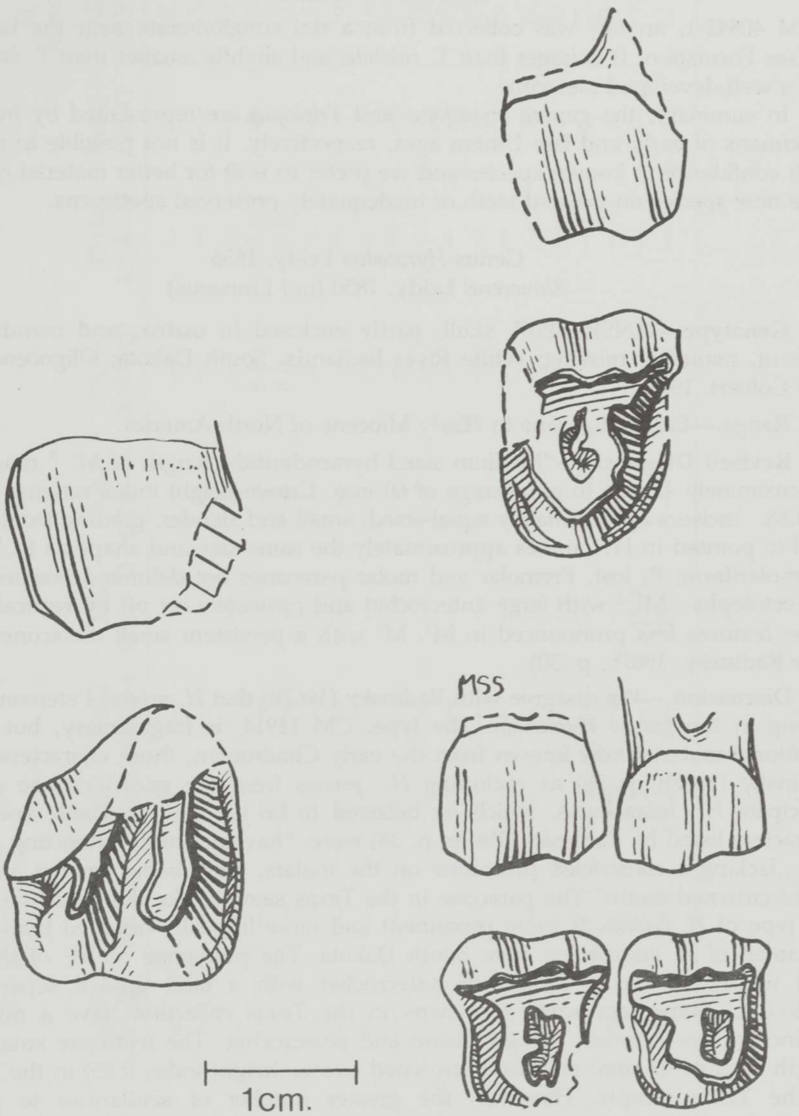

Fig. 15.—?*Triplopus* sp. TMM 42258-1. L P^3–P^4, R P^4, R M^3. Candelaria local fauna, Colmena Tuff.

Candelaria local fauna
Figure 15

TMM 42258-1, a series of upper teeth (fig. 15), was collected from the Colmena Tuff near the mouth of Capote Creek in the Vieja area. All the teeth are incomplete; however, they appear to belong to a species of *Triplopus*, perhaps close to *T. implicatus*. The M^3 is foreshortened, with the metacone depressed lingually as in the type of *T. obliquidens*. The genus *Triplopus* sp. should be added to table 1, table 2 (lower sorted facies), and table 14 of Wilson (1977b).

Big Bend National Park

TMM 40842-1, an M^3, was collected from a red conglomerate near the base of the Chisos Formation. It is larger than *T. cubitalis* and slightly smaller than *T. implicatus*; it has a well-developed metacone.

In summary, the genera *Hyrachyus* and *Triplopus* are represented by fragmentary specimens of early and late Uintan ages, respectively. It is not possible to refer them with confidence to known species and we prefer to wait for better material rather than base new species on isolated teeth or inadequately preserved specimens.

Genus *Hyracodon* Leidy, 1856
Rhinoceros Leidy, 1850 (not Linnaeus)

Genotype.—ANSP 10517, skull, partly enclosed in matrix, and mandible; skull present, mandible missing; White River badlands, South Dakota; Oligocene (Gillette and Colbert, 1976).

Range.—Early Oligocene to ?Early Miocene of North America.

Revised Diagnosis.—"Medium sized hyracodontids: length of M^{1-3} ranging from approximately 47 mm to an average of 60 mm. Crown-height index ranging from 0.65 to 0.88. Incisors approximately equal-sized, small and slender, grading from spatulate at $I\frac{1}{1}$ to pointed in $I\frac{3}{3}$. Canines approximately the same size and shape as $I\frac{3}{3}$. Premolars submolariform; P_1 lost. Premolar and molar paracones not delimited posteriorly from the ectolophs. M^{1-2} with large antecrochet and protocone set off by vertical grooves; these features less pronounced in M^3. M^3 with a persistent small metacone" (in part after Radinsky, 1967b, p. 30).

Discussion.—We disagree with Radinsky (1967b) that *H. primus* Peterson does not belong in the genus *Hyracodon*. The type, CM 11914, is fragmentary, but with the additional material now known from the early Chadronian, those characters listed by Radinsky (1967b, p. 38) as excluding *H. primus* from the genus can be shown to anticipate *H. nebraskensis*, which he believed to be the type and sole species. The characters listed by Radinsky (1967b, p. 38) were: "having a more projecting paracone, and...lacking a constricted protocone on the molars, and...being smaller and having lower crowned teeth." The paracone in the Texas sample, like the paracone on M^2 of the type of *H. primus*, is more prominent and more lingually oriented than that of a specimen of *H. nebraskensis* from South Dakota. The protocone on M^1 of the type is well worn and has a prominent antecrochet with a faint groove separating the protocone. Some less worn specimens in the Texas collection have a much more distinct groove between the protocone and antecrochet. The teeth are smaller (M^{1-3} length approx. 47 mm) and lower crowned (crown-height index 0.65) in the type than in the Texas sample. However, the greater number of similarities to *Hyracodon* outweighs more projecting paracones, smaller size, and lower crown, especially when these characters can be shown to be less distinctive with intermediate forms.

Hyracodon primus Peterson 1934
Porvenir local fauna
Figures 16–19, Tables 4–7

Type.—CM 11914, fragment of right maxillary with posterior part of P^4, broken M^1, M^2, and base of M^3; Duchesne River Formation, Lapoint Member, Uinta County, Utah.

Referred material.—TMM 40203-6, left maxillary with P^2–M^3 and right P^2. 40203-50, right maxillary fragment with P^4, M^1–M^3. 40492-20, right P^1. 40688-79, left P^1. 40492-29, right P^1–P^2. FMNH PM 92, left maxillary with M^1–M^1. FMNH PM 105, right M^2–M^3. FMNH PM 12, right maxillary with dP^2–dP^4. FMNH PM 140, right maxillary fragment with M^2–M^3. TMM 40203-45, left M^2. TMM 40203-30, right M^3.

Table 4. Measurements of upper teeth of *Hyracodon primus* and *H. petersoni* from Texas.

		H. primus											*H. petersoni*
		TMM 40203-50 R	TMM 40203-6 L	TMM 40203-50	FMNH PM 92	FMNH PM 105	TMM 41256-4	TMM 40203-30	TMM 40203-45	TMM 40492-20	TMM 40688-79	FMNH PM 12	TMM 42156-4
P^1–M^3		—	—	—	—	—	—	—	—	—	—	—	102.5
P^1–P^4		—	—	—	—	—	—	—	—	—	—	—	53.7
M^1–M^3		47.7 @	—	—	—	—	—	—	—	—	—	—	55.0
P^1	L	—	—	—	—	—	—	—	—	8.8	8.6	—	11.1
	W	—	—	—	—	—	—	—	—	8.0	8.9	—	11.0
P^2	L	10.1	10.0	—	—	—	—	—	—	—	—	—	14.5
	W	11.9	11.4	—	—	—	—	—	—	—	—	—	16.5
P^3	L	10.6	—	—	—	—	—	—	—	—	—	—	16.2
	W	15.0	—	—	—	—	—	—	—	—	—	—	18.8
dP^3	L	—	—	—	—	—	—	—	—	—	—	—	14.9
	W	—	—	—	—	—	—	—	—	—	—	—	15.4
P^4	L	13.0	—	—	—	—	—	—	—	—	—	—	17.4
	W	17.5	—	—	—	—	—	—	—	—	—	—	19.3
M^1	L	—	—	14.8	—	—	16.7	—	—	—	—	—	19.6
	W	—	—	17.1	—	—	17.3	—	—	—	—	—	20.7
M^2	L	16.9	—	17.2	18.3	18.0	—	—	17.0	—	—	—	22.7
	W	18.5	—	18.6	20.4	19.8	—	—	18.5	—	—	—	23.6
M^3	L	14.4	16.1	—	15.0	16.3	—	15.5	—	—	—	—	17.0
	W	18.1	17.8	—	18.4	19.2	—	18.5	—	—	—	—	22.7

TMM 41256-4, right M^1. FMNH PM 75, right M^3. FMNH PM 135, M^2 and left mandible fragment with posterior root of dP_1, dP_2–dP_4. TMM 40210-5, fragment P^4. TMM 40203-21, mandible with left I_3, C, P_2–M_2, roots of M_3, right alveoli of I_1–I_3 and C, P_2–P_3, fragment P_4, roots M_1–M_3. TMM 40731-3, left mandible fragment with P_2–M_2. TMM 40688-2, left mandible fragment with external part of M_1, M_2–M_3. TMM 40211-1, right mandible fragment with P_4, M_1. TMM 41216-7, left mandible fragment with M_2–M_3. TMM 40202-4, right mandible fragment with P_4, M_1. FMNH PM 23, P_4. TMM 40688-82, M_1. TMM 40688-51, fragment of M_2, M_3. TMM 40203-48, mandibular symphysis with roots of right I_1–I_3, C, roots of left I_1–I_2, C. Several lower jaw fragments with isolated teeth of uncertain position in the collection of FMNH.

Stratigraphic position.—Within the lower 100 ft (30.4 m) of the Chambers Tuff, or beneath the lower marker bed (Wilson, 1977b, table 4); less than 5 ft (1.5 m) below the lower marker bed at Red Mound north of Big Cliff, TMM 40992 (Wilson, 1977b, table 5); between 0 and 88 feet (0–26.8 m) above the lower marker bed, in the "Blue Cliff horizon" of the field notes of Bryan Patterson in the Field Museum of Natural History, Chicago (Wilson, 1977b, table 6), and between 25 and 42 ft (7.6–12.8 m) above the Buckshot Ignimbrite near Adobe Springs. All these sites are in the Chambers Tuff and part of the Porvenir local fauna. Approximately 62 ft (18.9 m) below the salmon-red marker bed in the Reeves Bonebed (TMM 40688), upper part of the Chambers Tuff, Vieja Group, and part of the Little Egypt local fauna (Wilson, 1977b, table 8), Brewster County, Texas. Within 200 ft (60.9 m) of the base of the Huelster Formation, northern Davis Mountains (Wilson, 1977b, p. 24).

Age.—Early Chadronian.

Revised diagnosis.—A small species of *Hyracodon*, length M^1–M^3 approximately 47 mm. Crown-height index 0.65. Upper incisors unknown, lower incisors as known from alveoli approximately equal in size. Upper canine unknown, lower canine slightly larger than I^3. Premolars premolariform. P^3–P^4 with cristae. P_1 lost. M^1 with large antecrochet and protocone set off by a vertical groove. M^3 with metacone.

Description.—The upper incisors and canine are unknown. An isolated P^1, TMM 40492-20 (fig. 16) is referred to *H. primus* with confidence. It is triangular; the paracones and metacones are slightly separated externally by a shallow groove. An internal ridge or crista forms an incipient metaloph opposite the shallow groove. A very shallow groove separates an incipient parastyle at the anterior margin of the tooth. A very short anterointernal cingulum is present internal to the parastyle. The cingulum does not extend internal to the protocone. The protocone is a slightly expanded portion of a crescentic ridge that forms the internal margin of the tooth. It originates between the bases of the parastyle and paracone but is not joined to either in an early wear stage. The internal crescentic ridge does not join with the median crista or metaloph. The P^2 is a larger tooth (fig. 16). A more developed protocone gives a more rectangular shape to the tooth. The ectoloph has prominent parastyle, paracone, and metacone. A crescentic protoloph extends around the anterior and internal portions of the tooth and connects with the metaloph in the middle part of the crescent. In a worn stage, the posterior part of the crescent connects with the metacone. Both anterior and posterior fossettes are closed. The ectolophs on P^3 and P^4 have prominent parastyles, paracones, and metacones. A crista is present on both P^3 and P^4. On P^3 the protoloph joins the metaloph to form an anterior fossette; on P^4 the protoloph remains separate.

The crista is absent on M^1, as in the type (FMNH 11914), but is present on P^3 and M^3. The parastyle on the molars is not as bulbous as in *Hyrachyus*. It is compressed against the paracone and is more elongate in a labial direction rather than in an anterior direction as in *H. petersoni*. The posterior extension of the ectoloph on M^3 is somewhat variable; on TMM 40203-50 it is long near the crown, whereas on TMM 40203-6 it is short. Both specimens are from the same stratigraphic level.

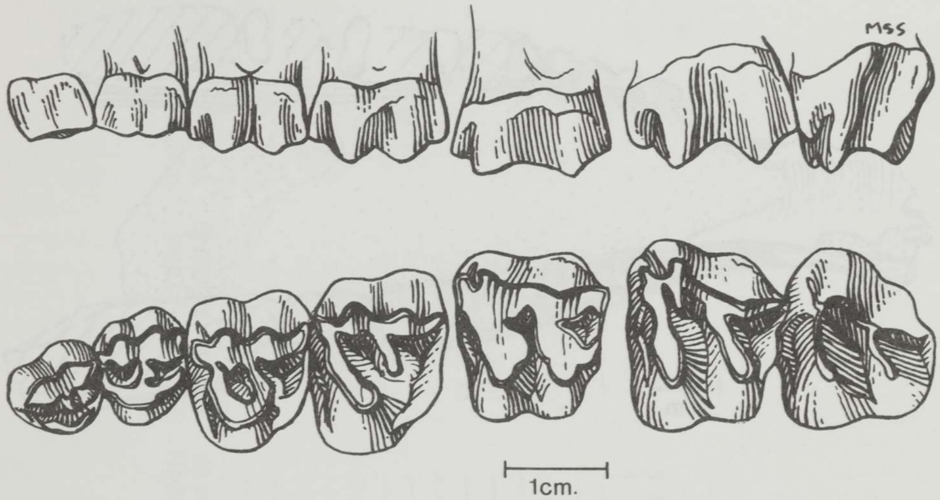

Fig. 16.—*Hyracodon primus*, TMM 40492-20 P^1 reversed, TMM 40203-6 P^2–M^3. Lateral and occlusal views. Porvenir local fauna, Chambers Tuff.

The cristae on M^2 and M^3 gradually become less prominent toward the base of the teeth and are lost in badly worn teeth. Similarly, the groove between the protocone and the antecrochet becomes less distinct toward the base of the tooth.

FMNH PM 12 is a fragmentary upper milk dentition. The internal half of dP^2 shows the protocone without a groove separating it from the separate parastyle. The dP^3 has a large, bulbous, and distinctly separate parastyle. The paracone is high and sharp and has a prominent crista. There is a prominent groove on the anterior side of the tooth labial to the protocone. The ectoloph on M^3 is oriented almost parallel to the midline whereas on dP^4 it is oriented more diagonally but not as markedly as on M^3. There are two distinct grooves that separate the protocone on dP^4. The anterior groove on the protoloph is sharp and extends almost to the summit of the unworn protocone. The parastyle of dP^4 is bulbous and more similar to that of *Triplopus*.

The best preserved lower jaw is TMM 40203-21 (fig. 17), in which the anterior part of the jaw contains alveoli for three incisors and the canine on the right side and I_2 and the canine on the left. The left canine is displaced, masking the other alveoli. The canines were larger than I_3 and, judging by the size of the alveoli, the incisors decreased in size toward the midline. Since the crowns of the incisors are not preserved, their shape is not known. Although worn, the crown of the canine appears to have been blunt. The canine is crowded directly behind I_3, and a long diastema (approximately 22 mm) separates it from P_2.

An isolated symphysis, TMM 40203-48, is identified as *H. primus* because a rather large canine is present posterior to I_3. The roots of the other right incisors are present, but the left side is broken diagonally across the symphysis so that roots of only two incisors are present.

P_2 and P_3 are present only in TMM 40203-21 and are so worn that very little of the occlusal pattern is left (fig. 17). There is no alveolus for a dP_1. The occlusal pattern of P_4–M_3 does not differ from that of *H. nebraskensis*. Only one Texas specimen, TMM 40731-3, shows any indication of labial or lingual cingula, and those are slight

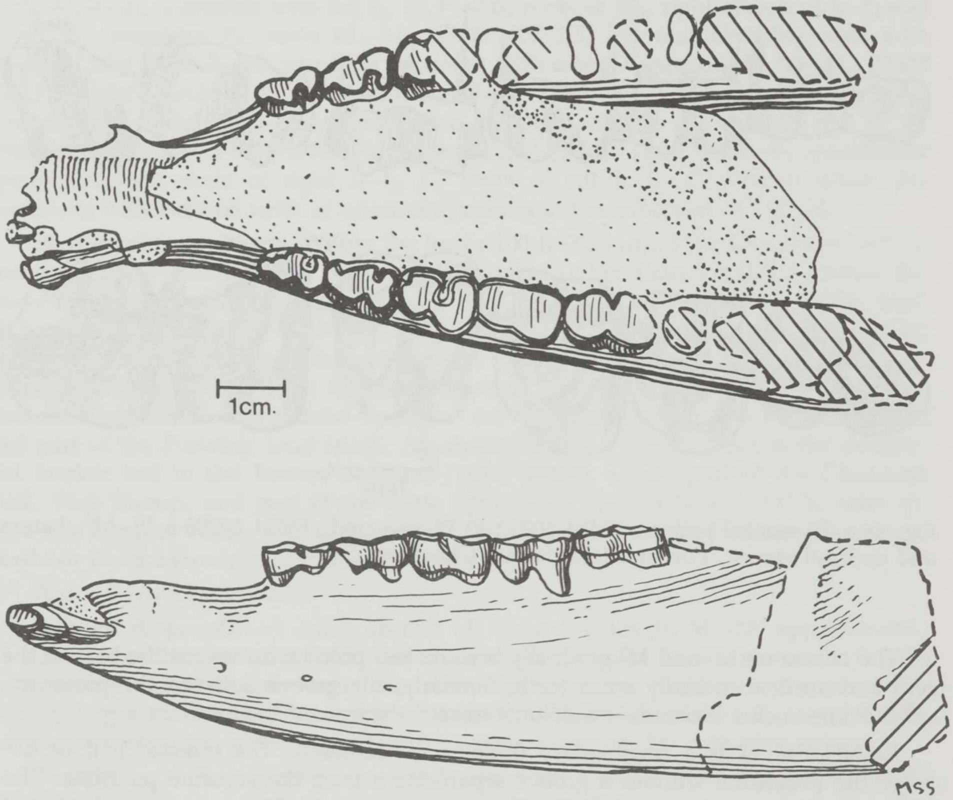

Fig. 17.—*Hyracodon primus* Peterson. TMM 40203-21. Occlusal view I_3, C, P_2–M_2. Lateral view C, P_2–M_2. Porvenir local fauna, Chambers Tuff.

compared to *H. nebraskensis*. The teeth of *H. primus* are much lower-crowned than those of *H. nebraskensis*. On TMM 40731-3 the height of the metaloph of P_4 is 12 mm, as compared to more than 18 mm for a slightly worn specimen of *H. nebraskensis*. Measurements are given in table 5.

The upper and lower milk dentition of *Hyracodon* have recently been fully described by Tanner and Martin (1972), and nothing can be added to their description. Two Texas specimens from the collection of the Field Museum of Natural History are shown in figures 18 (FMNH PM 12, table 4) and 19 (FMNH PM 135, table 5).

Discussion.—*Hyracodon primus* was first described by Peterson (1934) who stated: "the teeth agree most closely with those in *Hyracodon petersoni* Wood, except the less hypsodont crowns; the more prominent external cingulum of P^4, M^1 and M^2; and the greater convexity of the posterior portion of the ectoloph on P^4 and M^1." The external cingula on the molars of the Texas sample vary from absent to weak to moderate. When present, they are stronger on M^1 and M^2, as on the type, CM 11914. If a larger sample from Utah were available, the prominence of the crista would in all probability vary as it does in the Texas sample.

Table 5. Measurements of lower teeth of *Hyracodon primus* from Texas.

		TMM 40203-21	TMM 40731-3	TMM 40688-2	TMM 40202-4	TMM 40211-1	FMNH PM 68	FMNH PM 88	FMNH PM 23	TMM 40688-82	FMNH PM 135	TMM 41216-7
P_2	L	10.8	—	—	—	—	—	—	—	—	—	—
	W	7.4	—	—	—	—	—	—	—	—	—	—
dP_2	L	—	—	—	—	—	—	—	—	—	10.3	—
	W	—	—	—	—	—	—	—	—	—	6.2	—
P_3	L	12.5	—	—	—	—	—	—	—	—	—	—
	W	8.9	—	—	—	—	—	—	—	—	—	—
dP_3	L	—	—	—	—	—	—	—	—	—	13.7	—
	W	—	—	—	—	—	—	—	—	—	7.9	—
P_4	L	12.6	14.2	—	13.4	14.5	—	—	14.3	—	—	—
	W	9.9	10.3	—	9.6	10.0	—	—	10.9	—	—	—
dP_4	L	—	—	—	—	—	—	—	—	—	13.8	—
	W	—	—	—	—	—	—	—	—	—	8.5	—
M_1	L	13.7	16.0	15.3	14.8	15.4	—	—	—	14.2	—	—
	W	10.0	10.2	10.2	9.9	10.0	—	—	—	9.4	—	—
M_2	L	15.8	16.8	16.4	—	—	—	15.0	—	—	—	18.9
	W	10. 2 @	10.5	—	—	—	—	10.0	—	—	—	12.5
M_3	L	—	—	17.3	—	—	18.0	—	—	—	—	18.3
	W	—	—	10.3	—	—	11.2	—	—	—	—	10.6

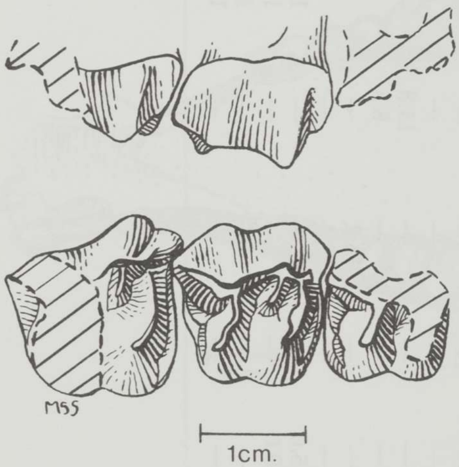

Fig. 18.—*Hyracodon primus*, FMNH PM 12. dP^{2-4}. Lateral and occlusal views. Porvenir local fauna, Chambers Tuff.

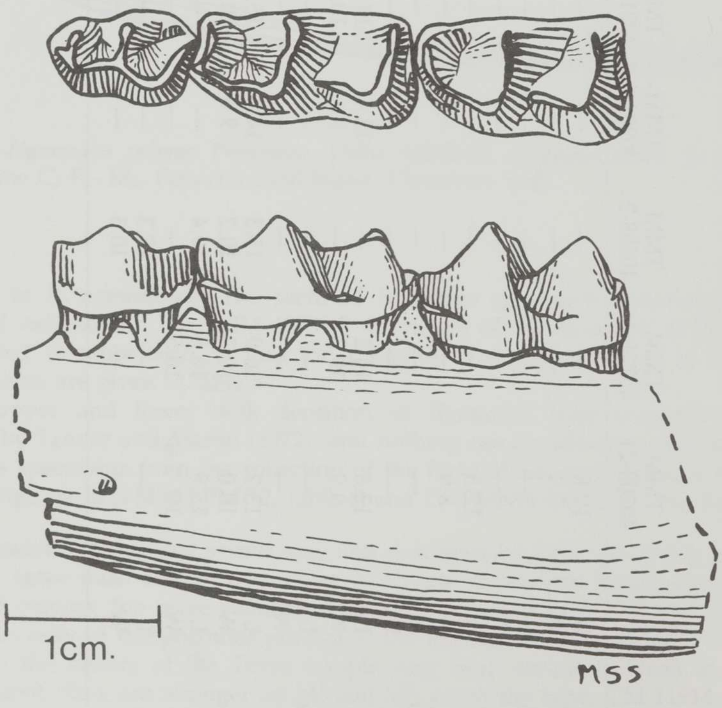

Fig. 19.—*Hyracodon primus*, FMNH PM 135. DP_{2-4}. Occlusal and lateral views. Porvenir local fauna, Chambers Tuff.

Radinsky (1967b, p. 38) suggested that "*Hyracodon primus* appears to be closest to *Triplopus,* but may represent a different genus." The Texas sample cannot belong to *Epitriplopus* because of the presence of a metacone on M^3 and the presence of the crista on M^2. *Epitriplopus* has a very concave ectoloph on M^1 and very molariform premolars, characters not found in *H. primus. H. primus* from Texas has lost P_1, at least in the adult stage, whereas *Triplopus* and *Epitriplopus* as diagnosed by Radinsky (1967b) have an unreduced dentition. The crown-height index for *Triplopus* as given by Radinsky averages 0.61 whereas in *H. primus* it is 0.65.

Comparative measurements for other species of *Hyracodon* are given in table 6 and statistical data for the Texas sample of *H. primus* are given in table 7. A comparison shows that the Texas form is the smallest known species of *Hyracodon* for which measurements are known. Tanner and Martin (1976) describe *H. doddi* based on USNM 11066, a right P^4–M^2. Their table 1 gives measurements for M^1–M^3 instead of P^4–M^2, which is apparently a *lapsus.*

This taxon should be added to tables 3 through 9 and table 14 of Wilson (1977b).

Radinsky (1967b) recognized two genera of North American hyracodontids in the late Eocene, *Triplopus* and ?*Forstercooperia.* The latter is a large form and is as yet not recognized in the Texas collection. In spite of the uncertain stratigraphic position of some specimens, Radinsky (1967b) believed that *Triplopus* characterized all of the late Eocene. A small species, *T. cubitalis,* and a larger species, *T. implicatus,* both were recognized in the late Eocene. A third species, *T. obliquidens,* was hesitantly recognized by Radinsky (1967b) because it overlapped in size and some other characters with *T. implicatus.* All three species occur in the early part of the late Eocene or Uinta B. Only a few specimens are known from the late part of the late Eocene or Uinta C. *T. rhinocerinus* and *Epitriplopus uintensis* are the only taxa recognized by Radinsky (1967b). The latter is distinguished primarily by the absence of a metacone on M^3.

Hyracodon primus of the early Chadronian is approximately the same size and has approximately the same crown height as *T. rhinocerinus* of the late Eocene, Uinta C. *T. rhinocerinus* appears to be a progressive form because of its comparatively large size, higher crowns, and molariform P^2. The P^2 of *Hyracodon primus* does not have separate protolophs and metalophs and would be regarded as a conservative or retarded form in terms of the nomenclature used by Radinsky (1963) for describing the premolars in tapiroids. The premolars of *H. primus* appear to be more similar to those of *T. cubitalis,* and we would, therefore, expect that *H. primus* was derived from a small, conservative, late Eocene triplopid. Such a form is, as yet, hypothetical.

The P^2 of *Hyracodon primus* is closer to the stage of development of P^1 of *H. arcidens* (PU 12518) as illustrated by Sinclair (1922). The P^4 of *H. primus* on both the type specimen (CM 11914) and TMM 40203-6 have an occlusal pattern like the P^4 of PU 12687 illustrated by Sinclair (1922, fig. 2b) and identified by him as *H. nebraskensis.* Sinclair (1922) used the character "transverse valley of P^4 blocked" as characteristic of *H. nebraskensis.* If that character were used alone, the Texas sample could be referred to *H. nebraskensis.*

Peterson described three medium-small ceratomorphs from the Duchesne River Formation of Utah. The first was a lower jaw fragment with P_3–M_2 (CM 11762), the type of *Mesamynodon medius* (Peterson, 1931). The second was an upper jaw fragment with P^3–M^2 (CM 11915), the type of *Epitriplopus medius* (Peterson, 1934). The third was an upper jaw fragment with P^4–M^2 (CM 11914), the type of *Hyracodon primus* (Peterson, 1934). The taxonomic portion concerning these taxa in Scott's (1945) monograph on the fauna of the Duchesne River Oligocene is rather contradictory and difficult to interpret. On page 247 he regretted Peterson's choice of the name

Table 6. Comparative measurements of upper teeth of various species of *Hyracodon*.

		Lambe (1908)		Scott (1941)		Troxell (1921)		Wood (1926)	Tanner & Martin (1976)
					YPM 11174	YPM 11173	YPM 11169		
		primus Type CM 11914	*priscidens*	*nebraskensis*	*arcidens minimus*	*leidyanus*	*selenidens*	*petersoni* Type CM 3572	*doddi* USNM 1106
P^1–M^3		—	—	122	129 est	142 est	110 est	—	—
P^1–P^4		—	62	66	67	74	57	53.8	—
M^1–M^3		—	62	61	—	—	—	52.0	—
P^1	L	—	12.3	11	13	14	11	10.7	—
	W	—	13.5	—	14	16	12	11.0	—
P^2	L	—	16	16	16	18	14	13.6	—
	W	—	20	—	19	21	16	15.2	—
P^3	L	—	16.8	19	18	21	15	14.4	—
	W	—	21.7	—	23	25	19	18.5	—
P^4	L	—	17.3	20	20	22	16	14.7	15.3
	W	—	23	—	26	27	21	20.6	22.1
M^1	L	—	22	20	—	24	19	17.3	16.4
	W	—	23.2	—	—	25	21	20.2	20.5
M^2	L	17.5	23	23	—	27	20	18.5	—
	W	17.5	24.5	—	—	27	21	21.7	22.6
M^3	L	—	19.5	20	—	—	17	16.2	—
	W	—	24	—	—	—	21	22.1	—

Table 7. Statistical data for upper teeth measurements of *Hyracodon primus* from Texas.

		N	OR			N	OR
M^1–M^3		1	47.7 @				
P^1	L	1	8.8	M^1	L	3	14.8–17.0
	W	1	8.0		W	3	16.5–17.3
P^2	L	2	10.0–10.1	M^2	L	4	16.9–18.3
	W	2	11.4–11.9		W	4	18.5–20.4
P^3	L	1	10.6	M^3	L	5	14.4–16.3
	W	1	15.0		W	5	17.8–19.2
P^4	L	1	13.0				
	W	1	17.5				

Mesamynodon because he did not think the type lower jaw (CM 11762) had any relationship to *Amynodon*. We agree with this conclusion. Scott continued under the heading *Mesamynodon*:

> In the posthumous paper, already referred to, Peterson proposed a new species of *Hyracodon*, naming it *H. primus*, the type of which is a fragment of an upper jaw, with p_4–m_3 (sic) in it, CM 11,914. In this maxillary, only m_2 (sic) is complete, the other teeth having lost more or less of their crowns and m^3 is not included in figure 8 of Peterson's paper. A second, referred specimen, which Peterson probably never saw (CM No. 11,915) has enabled Mr. Horsfall to draw unbroken crowns of p^4 and m^1 and a nearly complete m^3, which lacks the postero-internal portion. The three specimens, upper teeth (no. 11,914 and 11,915) and lower jaw, type of *Mesamynodon medius* (no. 11,672) agree well in size and are probably referable to the same species. If so, the latter name must be used, as having priority.

The upper jaw fragment (CM 11915) described by Scott as "a second, referred specimen, which Peterson probably never saw," is the type of *Epitriplopus medius* Peterson, 1934. This is apparently the *lapsus* referred to by Radinsky (1967b, p. 29) as follows: "Scott (1945, pp. 247–249) recognized the species *E. medius* but in an apparent *lapsus* referred its type, C.M. No. 11915, to *Hyracodon primus*, another Duchesnean hyracodontid species." This statement by Radinsky appears to be a misinterpretation of Scott, because Scott (1945, p. 247) placed "*Hyracodon* Peterson (*nec* Leidy) Ann. Carnegie Mus. 23:388, 1934" under *Mesamynodon*. In addition, on the same page Scott stated that *Mesamynodon* should have priority.

We therefore believe that, at least at one time during the preparation of his 1945 manuscript, Scott intended to synonymize all three species under *Mesamynodon*. However, in an apparent *lapsus*, Scott did not mention that CM 11915 is the type of *Epitriplopus medius*, and on pages 248–249 he retained *Epitriplopus medius*. Furthermore, figure 5, plate 2 of Scott (1945) is recognizable, in part, as CM 11915, although he did not identify the specimen in his "Explanation of the Plates" and referred to the figure only as "*Mesamynodon medius*; upper cheek-teeth, crown view, X 6/5." A careful examination of this figure leads us to suspect strongly that the drawing is a composite consisting of the P^3 and P^4 of CM 11915, the M^2 reversed of CM 11914, and the M^2 of CM 11915 drawn to look like an M^3. The M^2 of CM 11915 does not have a crista, whereas the M^2 of CM 11914 does. We therefore conclude that Scott's (1945) *lapsus* consisted not in erroneous referral of *Epitriplopus medius* to *Hyracodon primus*, as stated by Radinsky (1967b), but in erroneous referral of that type to *Mesamynodon medius*.

Scott's reference to "a nearly complete m^3, which lacks the postero-internal portion" (Scott, 1945, p. 247) in the drawing by Mr. Horsfall of CM 11915 is another *lapsus* because CM 11915, as Peterson (1934, p. 387) correctly reported, contains only P^3–M^2. However, microscopic examination of M^2 of CM 11915 showed that the ectoloph is a fragment that did not appear to fit directly against the paracone. When

the ectoloph fragment was removed, a fit was found between it and the base of the tooth, but this leaves a 2 mm gap in the ectoloph enamel, which lengthens the M^2 ectoloph and makes it certain that *E. medius* is conspecific with *E. uintensis* as indicated by Radinsky (1967b). Figure 15 in Radinsky (1967b) is the most accurate drawing of CM 11915.

To complicate matters even further, in the list of the Duchesne River fauna, Scott (1945, pp. 212–213) "with some additions and corrections, from the posthumous paper by Peterson,..." listed all three species, *Hyracodon primus, Mesamynodon medius,* and *Epitriplopus medius*. On page 213 he stated: "Several of the genera are clearly more or less modified survivals from the Uinta, others are new and akin to, or even congeneric with White River forms, such as *Teleodus, Hyracodon,* and *Hyaenodon,* seemingly their first appearance in North America." At the top of page 214 Scott wrote: "All of the three families of Rhinocerotoidea, the Hyracodontidae, the Amynodontidae, and the Rhinocerotidae, appear to be represented in the Duchesne River fauna, though remains are insufficient for a generic determination in all of them. Peterson assigned certain fossils to the White River genus *Hyracodon,* and I have followed his example." Scott recognized the presence of *Hyracodon* in the Duchesne River fauna again on page 215: "It is a generally accepted principle that, in dealing with stratigraphic problems, greater weight should be given to forms which are newcomers than to persistent older forms. The Duchesne River fauna includes several species which are referred to White River genera, such as *Hyaenodon, Hyracodon, Teleodus...*" Both *Mesamynodon* and *Epitriplopus* were listed by Scott as members of the Duchesne River fauna, but were not mentioned as newcomers.

The type of *Mesamynodon medius* (CM 11762) has P_3–M_2. We agree with Scott (1945, p. 247) that the small fragment of the root of P_2 does not mean that P_2 was vestigial as Peterson (1931) wrote in the original description. The type of *M. medius* belonged to a much larger individual than the type of *Epitriplopus medius* (table 5). The types of *H. primus* (CM 11914) and *E. medius* (CM 11915) belonged to animals very close to the same size (table 6) and these, in turn, both fall within the size range of the Texas sample referred to *H. primus*. The type of *Mesamynodon medius* (CM 11762), however, is considerably larger than comparable teeth in the Texas sample of *H. primus* and also the type of *E. uintensis*. The type of *Mesamynodon medius* is from the Lapoint Member. Scott (1945) said that "The molars are very much the same as in *Hyracodon* and display no generic difference from it." Without more material than the type, we cannot offer a solution to the taxonomic position of *Mesamynodon medius*.

Epitriplopus medius is listed by Anderson and Picard (1972) as coming from both the Brennan Basin Member and the Lapoint Member of the Duchesne River Formation. However, Peterson (1934) lists the type and only specimen as having come from the "Randlett Horizon" at a locality two miles east of Randlett Point, Uinta County, Utah. To our knowledge, there is no other published evidence of the occurrence of *Epitriplopus medius*. Emry (1981) independently reached the same conclusion. If *Epitriplopus medius* is the same species as *E. uintensis,* this adds to the similarity of the faunas from the Randlett or Brennan Basin and Uinta C. Andersen and Picard (1972) also listed *Mesamynodon medius* as occurring in the Brennan Basin Member, but there is no published evidence for this occurrence. The type and only specimen mentioned by Peterson (1931) is from the Titanothere Quarry in the Lapoint Member.

Hyracodon petersoni Wood 1926
Coffee Cup local fauna
Figure 20, Table 4

Type.—CM 3572, skull fragment with I^1–I^3, C, P^1–M^3.

Referred material.—TMM 42153-4, skull fragment with P^1–M^3, and associated lower jaw fragment with partial M_2 and M_3. TMM 40501-1, M^1.

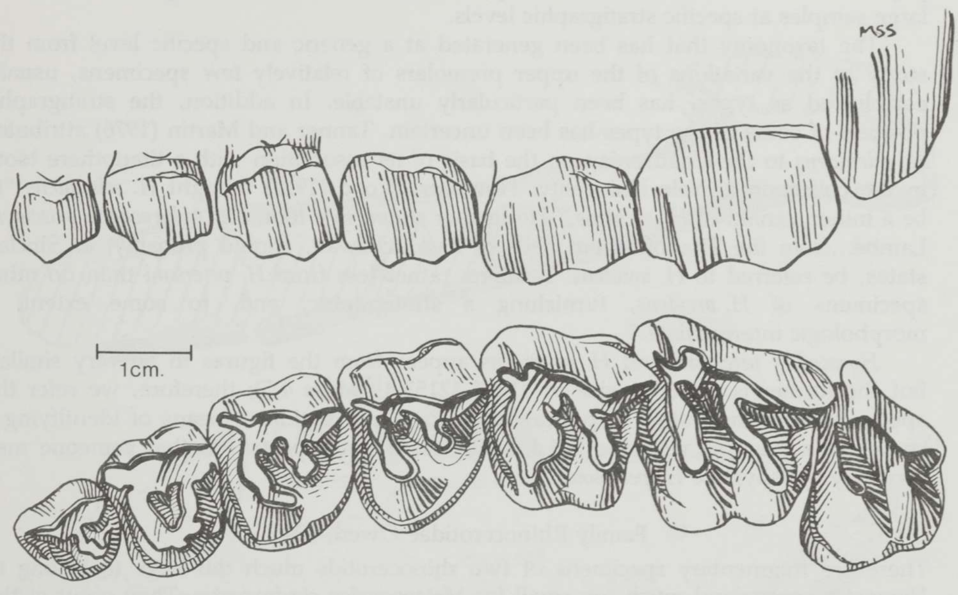

Fig. 20.—*Hyracodon petersoni*, TMM 42153-4. P^1–M^3. Lateral and occlusal views. Coffee Cup local fauna, Duff Tuff.

Stratigraphic position.—Within the lower 100 ft (30.4 m) of the Duff Tuff, approximately equivalent to the Bandera Mesa Member of the Devil's Graveyard Formation. Approximately 570 ft (173.7 m) above the Bracks Rhyolite, in Capote Mountain Tuff, Airstrip local fauna.

Age.—Chadronian.

Description.—A *Hyracodon* palate with complete dentition that is closest to *H. petersoni* in size and does not differ from it in any essential way. Crown-height index 0.79.

Discussion.—Radinsky (1976b) followed Scott (1941) in recognizing *H. nebraskensis* as the only species. Wood (1927) had recognized five species of *Hyracodon;* Sinclair (1922), four; and Troxell (1921), five. More recently Tanner and Martin (1976) described the species *H. doddi* and placed *H. petersoni* as a subspecies of *H. priscidens.* Tanner and Martin (1976) stated that "Four species of *Hyracodon* have been described from Chadronian sediments: *Hyracodon priscidens, H. selenidens, H. petersoni,* and *H. browni.*" They retained *H. primus* in the genus, but regarded the occurrence of *H. primus* in the Lapoint as "Upper Eocene." In addition, they rejected *H. browni* and in their figure 4 recognizec. *H. primus, H. selenidens, H. priscidens,* and *H. doddi,* the last three all occurring in the lower Oligocene.

Two diametrically opposed schools of thought concerning the taxonomy of *Hyracodon* are characterized by the conclusions of Scott (1941) and Radinsky (1967b) on the one hand, and Troxell (1921), Sinclair (1922), Wood (1927), and Tanner and Martin (1976) on the other. The former researchers recognized a single species, *H. nebraskensis,* for all of the Oligocene; the latter researchers recognized four or five and perhaps more. Unfortunately, neither school presented very convincing evidence to support one conclusion or the other. Large collections are known to be available, but to date nothing has been published that studies them from the point of view of

population statistics. It would certainly be helpful to know the range of variation of large samples at specific stratigraphic levels.

The taxonomy that has been generated at a generic and specific level from the study of the variations of the upper premolars of relatively few specimens, usually established as types, has been particularly unstable. In addition, the stratigraphic position of some of the types has been uncertain. Tanner and Martin (1976) attributed *H. selenidens* to the Chadronian on the basis of its association with a titanothere tooth in the collection at Yale University. However, Wood (1927) thought *H. selenidens* "to be a minor variant of *H. arcidens.*" He further stated in a footnote: "*Hyracodon priscidens* Lambe...from the Titanotherium Beds of Saskatchewan, should probably, as Sinclair states, be referred to *H. arcidens*. It differs rather less from *H. petersoni* than do other specimens of *H. arcidens*, furnishing a stratigraphic, and, to some extent, a morphologic intermediate."

Hyracodon petersoni and *H. priscidens* appear from the figures to be very similar, but the former is closer in size to TMM 42153-4 (tables 4,5); therefore, we refer the specimen from the Coffee Cup local fauna to *H. petersoni* as a means of identifying a comparable example with the full knowledge, if not expectation, that someone may someday synonymize *H. petersoni*.

Family Rhinocerotidae Owen, 1945

There are fragmentary specimens of two rhinocerotids much too large to belong to *Hyracodon primus* and much too small for *Metamynodon chadronensis*. They occur at the same stratigraphic level and belong to members of the Porvenir local fauna. Unfortunately, the fragmentary specimens do not preserve the parts that would permit certain identification. We have referred them questionably to previously described genera, knowing full well that better material may necessitate changes in their assignment. This seems to us the more prudent method because this family is already overburdened with taxa based on fragmentary specimens. We follow Radinsky (1966) in believing that the specialization of the anterior portions of the upper and lower jaws and the incisors and canines furnish the most distinctive characters for classification at a family level. We might add that the same specializations may prove to be the key at a generic level. Almost every possible combination of "primitive" or "advanced" condition for one or more upper premolars has been used by researchers to differentiate new taxa, a condition that hardly seems reasonable.

?*Caenopus* sp.
Porvenir local fauna
Figure 21

Referred material.—FMNH PM 141, fragmentary M^1–M^3; FMNH PM 39, ?P^4, fragmentary M^1, of right and left side but probably not same individual; FMNH PM 55, lower jaw fragment with roots of ?I_2, at least two alveoli posterior to ?I_2, roots of P_4–M_3, anterior premolars uncertain.

Stratigraphic position.—Below and above the lower marker bed, Chambers Tuff, Vieja Group. The position for FMNH PM 39 is listed as "Big Red Horizon" and that for FMNH PM 141 as "Blue Cliff Horizon" in field notes of Bryan Patterson and in Wilson (1977b, fig. 7). Porvenir local fauna.

Description.—The lower jaw fragment preserves the symphysis with the roots of two recumbent tusks (fig. 21). Presumably these are roots of I_2, but the anterior-most portion of the symphysis is missing so that any other alveoli are not present. There are at least two alveoli posterior to the roots of ?I_2 which would be for I_3 and the lower canine. A long diastema (25+ mm) separates the alveolus for the lower canine from the faint alveolus for a premolar. The anterior premolar alveoli are so faint that the number of premolars anterior to P_4 is uncertain. However, no matter their

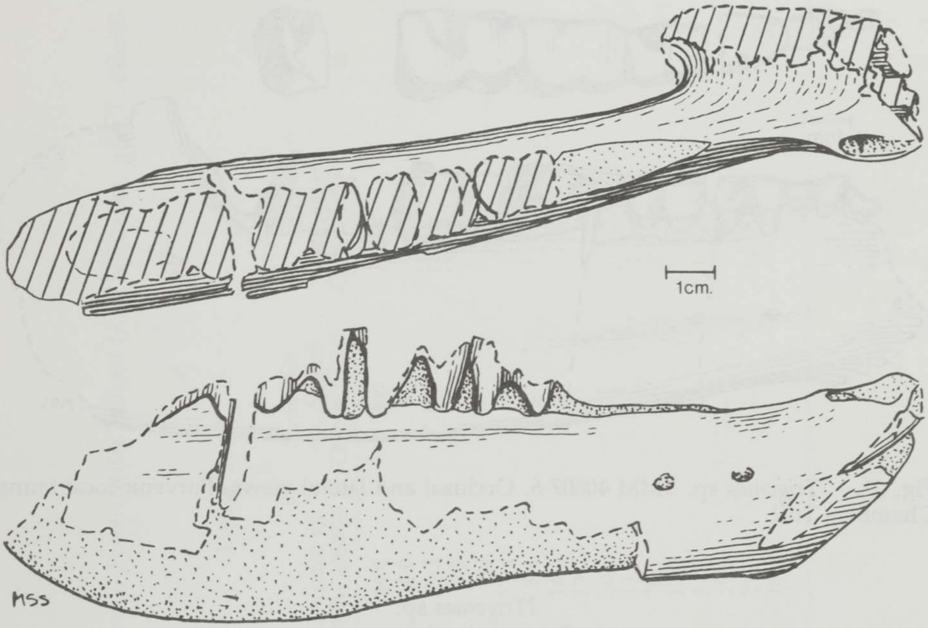

Fig. 21.—?*Caenopus* sp. FMNH PM 55. Dorsal and lateral views. Porvenir local fauna, Chambers Tuff.

number, the space occupied by those premolars was very short (27 mm est.) compared to that occupied by P_4–M_3 (90 mm est.).

Discussion.—The shortening of the premolars compared to the molars is a trend found in the family Amynodontidae and also in the early to late Oligocene genus *Ardynia* of Asia (Radinsky, 1967b). FMNH PM 55 is certainly not an amynodont, and the tusk-like ?I_2 is unlike *Ardynia* although the two may have been related prior to the Chadronian. Prior to our studies, several researchers had labeled FMNH PM 55 as *Caenopus*. If the species referred to it by Wood and Wood (1937) are valid, then *Caenopus dakotaensis* of the upper Oligocene, the type of which is AMNH 1110 (Osborn, 1898, fig. 39), does not show a shortening of the anterior premolars. The type specimen of *C. mitis* (AMNH 6325) is fragmentary and the lower jaw fragment has no teeth. Unfortunately, the lower jaw fragment has not been figured. However, if the procumbent tusk in the Texas specimen is I_2, as would be expected, then alveoli for I_3 and the canine are present and occur as in the genus *Caenopus* as defined by Wood (1927) and Scott (1941). The genus *Procaenopus premitis* (Figgins, 1934) has an upper premolar measurement of 84.3 mm (Figgins, 1934, p. 13) and is therefore much too large for a lower jaw the size of the Texas specimen. The same line of reasoning applies if FMNH PM 55 is compared to AMNH 6525, illustrated by Osborn (1898) as the cotype of *Aceratherium* = *Caenopus mitis*. Proper identification of the Texas form will have to await better material. We can only say that a rhinocerotid of small to intermediate size with enlarged lower tusks and reduced premolars was already present in very early Chadronian time.

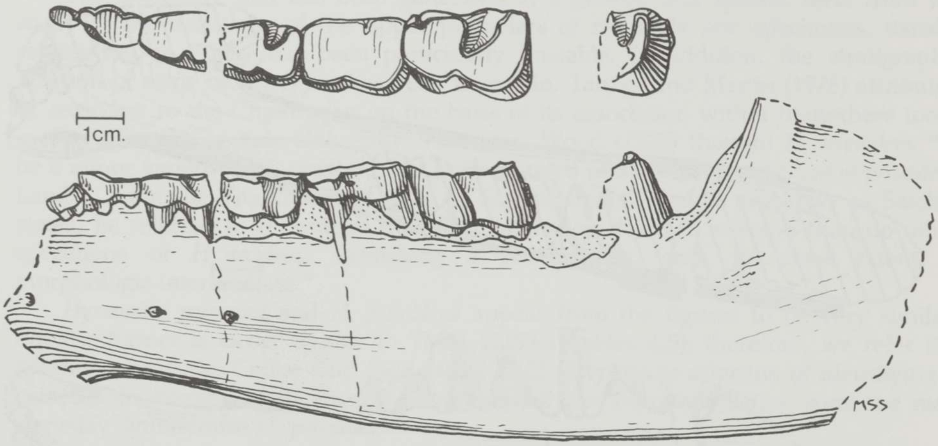

Fig. 22.—?*Trigonias* sp. TMM 40807-6. Occlusal and lateral views. Porvenir local fauna, Chambers Tuff.

?*Trigonias* sp.
Porvenir local fauna
Figure 22, Table 8

Referred material.—TMM 40688-33, maxillary fragment with alveolus for P^1, fragmentary P^2–M^1; TMM 40807-6, mandible with P_1–M_3; TMM 40807-1, mandible fragment with posterior half of ?M_1, ?M_2, and part of unerupted ?M_3; FMNH PM 87, mandible fragment with M_1; TMM 40113-1, mandible with roots of P_1–P_4, part of M_1–M_2, roots of M_3.

Stratigraphic position.—Both below and above the lower marker bed, Chambers Tuff, Vieja Group; Porvenir local fauna (Wilson, 1977b, fig. 7), Presidio County, Texas. TMM 40133-1 is from a pebble conglomerate just below the Whirlwind Breccia, upper Pruett Formation, Buck Hill Group, Brewster County, Texas.

Description.—The teeth of the maxillary fragment TMM 40688-33 are so badly worn that nothing is left of the occlusal pattern. However, the teeth are much too large for *Hyracodon primus*, and the premolar series is too long to be associated with FMNH PM 55, ?*Caenopus* sp.

The lower jaw, TMM 40807-6 (fig. 22) has a full dentition. The first premolar is very small (table 8) and is tilted anteriorly as though almost ready to be lost. Unfortunately, the symphysis is broken off too far posterior to preserve the roots of lower tusks if they were present. The occlusal surfaces of the lower teeth are so worn that no details of the pattern are preserved.

Discussion.—Tanner and Martin (1976) have erected the genus and species *Penetrigonias hudsoni* on the basis of USNM 62049, a P^2–P^4 from the upper part of the Chadron Formation of Nebraska. The pattern of the P^2 of the Texas *Hyracodon petersoni* is like the P^2 of *Penetrigonias* but P^3–P^4 are different. The Texas specimen lacks the hypocone on P^3–P^4 and has smaller premolars than *Penetrigonias*. The premolar series of TMM 40688-33 is too fragmentary and worn to compare with *Penetrigonias*. Tanner and Martin (1976, p. 213) suggest that *Penetrigonias* represented "a group of miniature rhinocerotoids with tooth characters resembling those of amynodonts." Because their only basis for comparison was the upper premolar series, we would like to point out

Table 8. Measurements of upper and lower teeth of ?*Trigonias* sp. from Texas, *Penetrigonias hudsoni* from Nebraska, and *T. osborni* var. *figginsi* and *T. taylori* from Colorado.

Upper Teeth

		TMM 40688-33	Tanner & Martin (1976) *Penetrigonias hudsoni* USNM 62049
P^2	L	15.7	13.2
	W	—	17.4
P^3	L	—	16.0
	W	—	18.8
P^4	L	22. @	15.2
	W	—	22.5

Lower Teeth

		?*Trigonias* sp. TMM 40807-6	*T. osborni* var. *figginsi* CMNH 951(1)	*T. taylori* CMNH 1029
P_1–M_3		134.0	200	190
P_1–P_4		54.9	82	80
M_1–M_3		79.5	115	108
P_1	L	8.0	—	—
	W	4.5	—	—
P_2	L	13.4	—	—
	W	8.1	—	—
P_3	L	14.1	—	—
	W	12.7	—	—
P_4	L	20.5	—	—
	W	13.9	—	—
M_1	L	20.1	—	—
	W	17.3	—	—
M_2	L	27.5	—	—
	W	19.5	—	—
M_3	L	29.5 @	—	—
	W	18.0	—	—

that the upper premolar series of *Amynodon advenus* from the late Eocene of Texas shows considerable variation (Wilson and Schiebout, 1981). The Texas specimen is much too small to be referred to any of the species of *Trigonias* described by Gregory and Cook (1928) from the Chadronian of Colorado.

Family *incertae sedis*
Genus *Toxotherium* Wood, 1961
Toxotherium hunteri Wood, 1961
Porvenir, Little Egypt, and Ash Spring local faunas

No new specimens that can be referred to this species have been found since Harris (1967) published on a lower jaw fragment from the Ash Spring local fauna and Schiebout (1977) published on *Schizotheroides jackwilsoni*. Some additional material that is tentatively referred to *Toxotherium* is described below.

Genus ?*Toxotherium* Wood, 1961
?*Toxotherium* sp. Wood, 1961
Figures 23–27, Table 9

Type.—NMC 8918, anterior half of right mandibular ramus with P_4–M_1.

Referred material.—FMNH PM 63, posterior part of skull with posterior part of alveolus for RP^4, fragmentary worn M^1, fragments and alveoli of M^2 and M^3, and well preserved basicranium; TMM 40283-17, RP^2 or P^3; TMM 40283-148, badly worn LM^1 and fragment of LM^2; TMM 41929-1, badly fractured lower jaw fragment with parts of two teeth of uncertain position. The hypodigm of *Toxotherium hunteri* is given in Emry (1979).

Stratigraphic position.—FMNH PM 63 occurs in the "Blue Cliff Horizon" (Wilson, 1977b, fig. 7), Chambers Tuff, Vieja Group. TMM locality 40283 is at Ash Spring in the undifferentiated part of the Vieja Group, Chadronian. TMM locality 41929 is within 25 ft stratigraphically above the Cotter channels (fig. 1, locality H), Devil's Graveyard Formation, Brewster County, Texas.

Description.—Only the P^2 (TMM 40283-17) and the skull fragment (FMNH PM 63) are sufficiently complete to add new information. TMM 40283-17 consists of a fragment of a maxilla containing a tooth which, although we cannot be certain, appears to be the anteriormost premolar, which is probably P^2. This tooth is larger than the P^1 of *Hyracodon primus* and smaller than the P^2 of that taxon. Although part of the parastyle is broken off, the P^2 has a very definite anteroexternal orientation that is not present in either P^1 or P^2 of *H. primus*. There is a prominent anterior cingulum, but because the internal enamel face of the tooth is broken off, we cannot tell whether there was an internal cingulum around the protocone. The protoloph and ectoloph are the most prominent lophs. The external surface of the enamel of the ectoloph is incomplete, but there does not appear to be a sharp separation between the paracone and metacone. The metaloph appears as a wear surface on the internal side of the metacone. A crista extends from this wear surface to the protocone. Measurements of the tooth are given in table 9.

The skull fragment (FMNH PM 63) is tentatively identified as *Toxotherium* because the alveoli and tooth fragments in the alveoli are very close in size and tooth shape to those of TMM 40840-42. The maxillary bone of the latter is slightly larger than that of FMNH PM 63. The shape of the maxillary bone, the position of the anterior base of the zygomatic arch, and the position of the ventral edge of the orbit are the same in both specimens. Only fragments of the molars are preserved in the alveoli, the remainder having been broken away during burial in a rather coarse conglomerate. The right M^1 has a well worn protoloph, the anterior cingulum, and about half of the metaloph preserved. The parastyle and the posteroexternal corner of the ectoloph are worn off. The proto- and metalophs have an oblique orientation. Approximate

Table 9. Measurements of upper teeth of *Toxotherium hunteri*, ?*Toxotherium* sp., *Sianodon sinensis*, and *S. mienchiensis*.

		?*Toxotherium* sp.	*Toxotherium hunteri* Schiebout (1977)	*Toxotherium hunteri*	*Toxotherium hunteri* Emry (1972)		*Sianodon sinensis* Zdansky (1930)			*S. mienchiensis* Chow & Xu (1965)
		TMM 40283-17	TMM 40206-22	TMM 40840-42	USNM 244359	USNM 244358	Type	Cotype	Isolated teeth	PRC V 3021.2
P^2	L	8.3	—	—	—	—	—	11.5	—	—
	W	8.4	—	—	—	—	—	—	—	—
P^3	L	—	—	—	—	—	12.3	13.1	13.0	—
	W	—	—	—	—	—	16.3	16.9	16.6	—
P^4	L	—	—	9.4 m	—	—	14.8	15.5	15.7	—
	W	—	—	11.8	—	—	21.1	21.0	21.4	—
M^1	L	—	—	13.7	12.3	11.5	24.5 @	27.5	24.0	—
	W	—	—	13.9	12.2	12.1	25.0	24.9	25.2	—
M^2	L	—	—	18.2	14.8	—	29.0 @	32.5	—	—
	W	—	—	17.5 est	15.0 est	—	28.8	28.5	—	—
M^3	L	—	16.3	17.2	—	—	25.1	—	—	19.0 est
	W	—	18.1	20.2	—	—	27.8	—	—	21.0 est

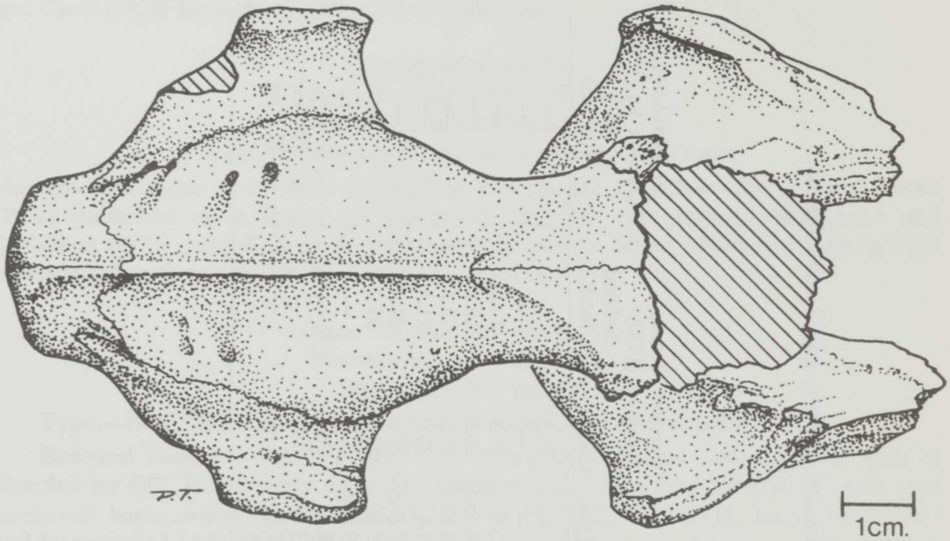

Fig. 23.—?*Toxotherium* sp. FMNH PM 23. Skull fragment, dorsal view.

measurements of M^1 are L 1.1 est, W 1.3 est. Only the central portion of the protoloph of M^2 is preserved. The posteroexternal and posterointernal portions of the base of M^3 are preserved and retain the enamel. The posteroexternal outline of the enamel shows that a metacone was present on M^3. This character eliminates the possibility that FMNH PM 63 belongs to *Epitriplopus*.

The median suture is visible as far posterior as the origin of the saggital crest on the dorsal surface of the skull (fig. 23). The crest is complete and forms an arc to the supraoccipital. The sutures between the frontals and parietals and grooves leading from these into the parietals are present on both sides of the saggital crest. The posterior groove extends onto the dorsal surface of the supraoccipital. The supraoccipital has a moderate overhang above the basiocciput. In lateral view (fig. 24), the most distinguishing feature is the opening for the ossified external auditory meatus. The postglenoid process is united by a suture to the external auditory tube. The suture lies in the middle portion of the tube and extends almost a third of the way down the posterior surface of the postglenoid process. The posterior contact of the tube with the mastoid process appears to be much less secure. A posttympanic process forms part of the anterior basal surface of the paroccipital process. The mastoid portion extends onto the posterior surface of the skull (fig. 25). A ridge on the ventral surface of the tube extends from the posteroexternal lip of the meatus to a small pit that probably held the cartilaginous attachment for the tympanohyal. The anteroexternal portion of the bulla is ossified and preserved (figs. 26, 27). It was not greatly inflated, as nearly as can be told from the remnant that is present on the right side. The petrosal is present and the foramen rotundum is visible. No other foramina are visible on the ventral surface of the petrosal. A shallow groove of undetermined significance passes around the internal surface of the petrosal.

The position of the right petrosal is different from that of the left petrosal, and the ossified portion of the bulla on the left side was removed accidentally during early

Fig. 24.—?*Toxotherium* sp. FMNH PM 23. Skull fragment, lateral view.

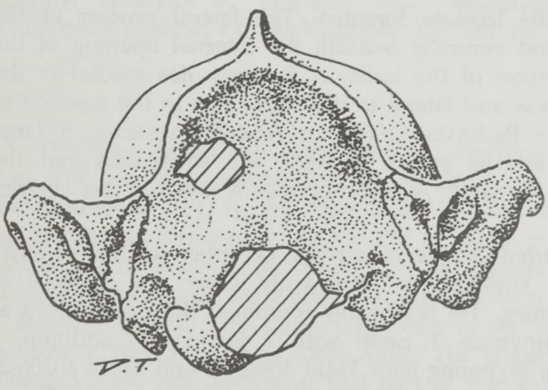

Fig. 25.—?*Toxotherium* sp. FMNH PM 23. Skull fragment, posterior view.

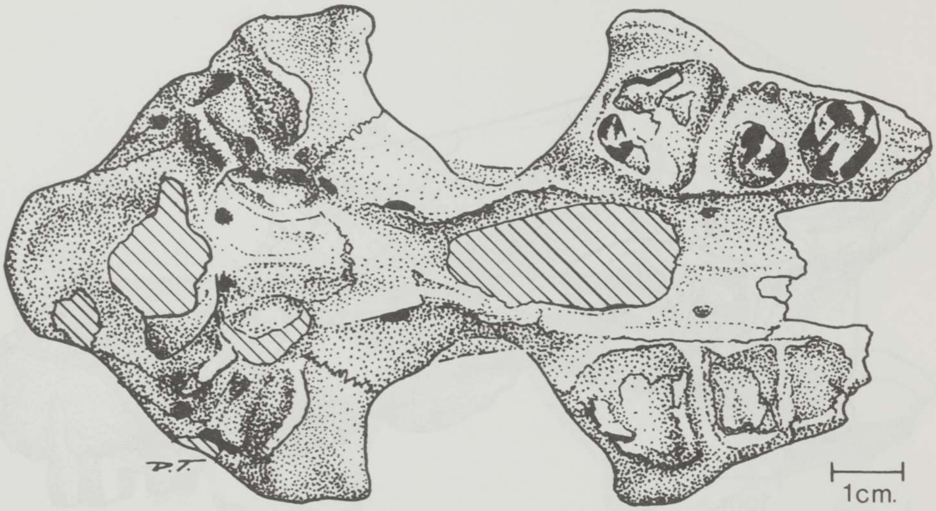

Fig. 26.—?*Toxotherium* sp. FMNH PM 23. Skull fragment, ventral view.

preparation. More of the lateral portion of the petrosal can be seen on the left side. Medial to the position of the squamosal-alisphenoid suture, a process extends laterally from the main body of the petrosal to articulate with the posterior end of the alisphenoid. The foramen ovale is lateral to this, a condition more similar to that in *Rhinoceros* than to that in *Amynodon*. A very thin process of the alisphenoid separates the foramen ovale from the middle lacerate foramen. The lateral process of the petrosal expands posterolaterally and ventrally beneath the internal opening of the meatus and forms the ossified portion of the bulla. A foramen lies medial to the medial end of the postglenoid process and lateral to the bulla. It is in the position of the "groove for artery" figured by Radinsky (1965) for *Heptodon posticus*. A large stylomastoid foramen is present on the suture between the squamosal and the mastoid on the posterior surface of the skull. A small foramen is situated just anterior to the hypoglossal foramen.

Discussion.—Emry (1979) reported on the occurrence of upper teeth of a small rhinocerotoid found at the same stratigraphic level with lower jaw material of *Toxotherium* at Flagstaff Rim, Wyoming. He reasonably identified the upper teeth as *Toxotherium* and went on to synonymize *T. woodi* with *T. hunteri*. In addition, a comparison of the upper teeth from Wyoming with TMM 40840-42 and TMM 40206-22 from Texas convinced him that they belonged to a single taxon. Schiebout (1977) was not aware of the upper teeth referred to *Toxotherium hunteri* by Emry (1979). The only teeth available in the Texas collection as of 1977 included the dP^2 and dP^3 (TMM 40283-100) and the permanent uppers, identified by Schiebout as *Schizotheroides*. These occurred at different localities and at different stratigraphic levels. At the present time, we are in agreement that the evidence presented by Emry (1979) can form the basis of a reasonable assumption and that it can be further interpreted. All of this, of course, depends on the discovery of an articulated skull and jaws with pertinent parts of the dentition.

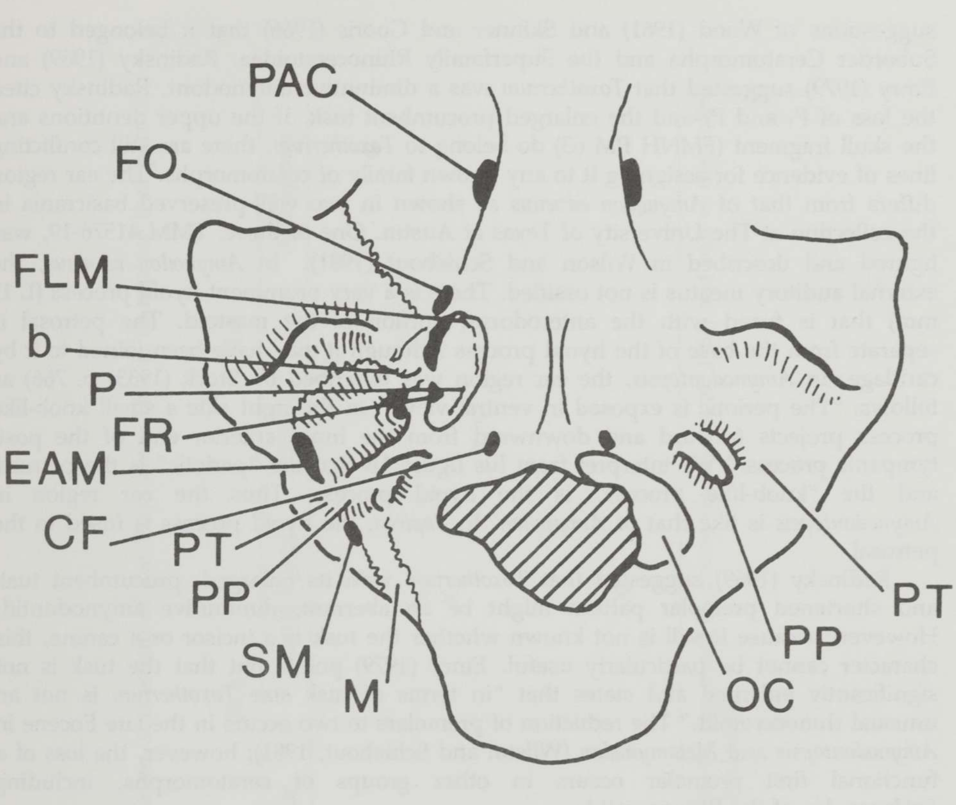

Fig. 27.—?*Toxotherium* sp. FMNH PM 23. Restoration of basicranium. b, ossified portion of bulla; CF, condylar foramen; EAM, external auditory meatus; FLM, foramen lacerum medius; FO, foramen ovale; FR, foramen rotundum; M, mastoid process; OC, occipital condyle; P, petrosal; PAC, posterior opening alimentary canal; PP, paroccipital process; PT, posttympanic process; SM, stylomastoid foramen.

The Texas material is more scattered stratigraphically than that from the Flagstaff Rim. The lowest occurrence is TMM 40206-22, an isolated M^3 from the lower part of the Chambers Tuff, or the "Big Red Horizon" of Bryan Patterson (Wilson, 1977b, fig. 7). The skull fragment, FMNH PM 63, came from the same general area, but from higher in the section, in the "Blue Cliff Horizon." Both specimens are from the Porvenir local fauna. TMM 40840-42, the specimen chosen by Schiebout as the type of *S. jackwilsoni*, came from Chalk Gap Draw in the upper part of the Chambers Tuff and belongs to the Little Egypt local fauna. The specimen described by Harris (1967) was collected from Ash Spring in that part of the Vieja Group where the igneous flows used to subdivide the Group are absent. The Ash Spring local fauna is believed to be the youngest in the Vieja Group, but this cannot be proven by superposition. Two other specimens from the Ash Spring locality which are tentatively identified as *Toxotherium* are a right ?P^2 (TMM 40283-17) and fragmentary left M^1 and M^2 (TMM 40283-148). A lower jaw fragment with badly preserved teeth from the middle part of the tooth row (TMM 41929-1) was found in the "upper red table silts" at the Cotter Ranch in the Green Valley area. All of these occurrences are in the Chadronian.

The fragmentary condition of what is known of *Toxotherium* has presented difficulties in assigning it to higher taxonomic units. Emry (1979) reviewed the

suggestions of Wood (1961) and Skinner and Gooris (1966) that it belonged to the Suborder Ceratomorpha and the Superfamily Rhinoceratoidea. Radinsky (1969) and Emry (1979) suggested that *Toxotherium* was a diminutive amynodont. Radinsky cited the loss of P_1 and P_2 and the enlarged procumbent tusk. If the upper dentitions and the skull fragment (FMNH PM 63) do belong to *Toxotherium*, there are still conflicting lines of evidence for assigning it to any known family of ceratomorphs. The ear region differs from that of *Amynodon advenus* as shown in two well-preserved basicrania in the collection at The University of Texas at Austin. One of these, TMM 41576-19, was figured and described in Wilson and Schiebout (1981). In *Amynodon advenus*, the external auditory meatus is not ossified. There is a very prominent hyoid process (L 17 mm) that is fused with the anterodorsal portion of the mastoid. The petrosal is separate from the base of the hyoid process although it may have been joined to it by cartilage. In *Amynodontopsis*, the ear region was described by Stock (1933, p. 766) as follows: "The periotic is exposed in ventral view. On the right side a small knob-like process projects forward and downward from the inner anterior end of the post-tympanic process." We interpret from his figure 1B that the "periotic" is the petrosal and the "knob-like process" is the hyoid process. Thus the ear region in *Amynodontopsis* is like that of *Amynodon*. In *Tapirus*, the hyoid process is fused to the petrosal.

Radinsky (1969) suggested that *Toxotherium* with its enlarged, procumbent tusk and shortened premolar pattern might be an aberrant, diminutive amynodontid. However, because it still is not known whether the tusk is a incisor or a canine, this character cannot be particularly useful. Emry (1979) points out that the tusk is not significantly enlarged and states that "in terms of tusk size *Toxotherium* is not an unusual rhinocerotoid." The reduction of premolars to two occurs in the late Eocene in *Amynodontopsis* and *Metamynodon* (Wilson and Schiebout, 1981); however, the loss of a functional first premolar occurs in other groups of ceratomorphs, including *Subhyracodon* of the Rhinocerotidae.

An ossified external auditory meatus and fragments of an ossified bulla are very rare in ceratomorphs. Strangely enough, this structure was preserved in one of the first Eocene forms to be described from North America, *Triplopus cubitalis* Cope, 1880. The presence of the meatus was used by Cope (1881, 1884) as a character for erecting the family Triplopidae. In 1884 (p. 680) he said:

> The *meatus auditorius externus* is large, and occupies only the posterior part of the space between the postglenoid and posttympanic processes. It is inclosed anteriorly and below by the border of a wide element which may be tympanic. It incloses the petrous bone below in a bulla....

The same structure is mentioned again by Osborn (1890, p. 529) and by Peterson (1919, pp. 135, 138), who compared the condition found in *Triplopus cubitalis* and *Prothyracodon uintense* = *Epitriplopus uintensis*. Peterson proposed that *Triplopus* be placed in the subfamily Triplopodinae of the family Hyracodontidae. Radinsky (1967b, p. 8) stated:

> An ossified auditory bulla is known in only one specimen of *Triplopus cubitalis*, A.M.N.H. No. 5095. It is a thin sheet of bone that covers only half of the petrosal as seen in ventral view, and apparently is only loosly (*sic*) attached to the skull. It would be preserved only under the most favorable conditions of burial and fossilization. In the two specimens of *Prothyracodon obliquidens* that include the ear region, no tympanic is preserved in one, C.M. No 3201, and in the other, C.M. No. 11957, on one side only fragments of an ossified bulla appear to be present.

The presence of an ossified external auditory meatus in ?*Toxotherium* could be used to demonstrate a relationship with *Triplopus*. Certainly the size of *Toxotherium* is closer to that of *Triplopus*, although some amynodonts from the People's Republic of China are small, for example, *Sianodon mienchiensis*, *S. honanensis*, and *S. sinensis* (Chow and Xu, 1965). Comparative measurements given in table 9 show that

Table 10. Stratigraphic occurrences of ceratomorphs in the local fauna succession of the Vieja area. This is to replace that part of Table 14 in Wilson (1977b).

K-Ar dates	40.0	38.6	36.8		31.4
Local Faunas	Candelaria	Porvenir	Little Egypt	Airstrip	Ash Spring
Dilophodon cf. *D. leotanus*	X				
?*Triplopus* sp.	X				
Colodon cf. *hancocki*	X				
Colodon stovalli		X	X		
Hyracodon primus		X	X		
Hyracodon petersoni				X,X*	
?*Metamynodon mckinneyi*	X				
Metamynodon chadronensis		X			
?*Caenopus* sp.		X			
?*Trigonias* sp.		X			
Toxotherium woodi		X	X		X
?*Toxotherium* sp.		X			X

*Within the lower 100 ft. (30.4 m) of the Bandera Mesa Member of the Devil's Graveyard Formation (Stevens et al. 1984) and part of the Coffee Cup Ranch local fauna, which is approximately equivalent to the Airstrip local fauna.

Table 11. Stratigraphic occurrences of ceratomorphs in the local fauna succession of the Agua Fria-Green Valley areas.

K-Ar dates	48.6,45.8 42.9		41.7	31.6
Local Faunas	Whistler Squat	Serendipity	Skyline	Coffee Cup
?*Hyrachyus* cf. *H. modestus*	X			
Hyrachyus cf. *H. modestus*	X*			
?*Triplopus* cf. *T. implicatus*	X			
?*Triplopus* sp.		X		
Hyracodon petersoni				X
Amynodon advenus	X			
Metamynodon mckinneyi		X		
Amynodontopsis bodei			X	
?*Trigonias* sp.				X**
?*Toxotherium* sp.			X***	

*Big Yellow Sandstone Member, Canoe Formation, Big Bend National Park
**Just below Whirlwind Breccia, upper Pruett Fm. (Goldich & Elms, 1949)
***Cotter Channel

Toxotherium is smaller. *Triplopus* is a member of the family Hyracodontidae, and on the basis of the evidence known at present, we might refer to *Toxotherium* as a diminutive aberrant hyracodontid. We believe, however, that the evidence still is inconclusive and prefer to let *Toxotherium* remain *incertae sedis* within the superfamily Rhinocerotoidea.

SUMMARY AND CONCLUSIONS

Late Eocene ceratomorphs that were present in West Texas (tables 10, 11) include *Amynodon advenus, Metamynodon mckinneyi, Amynodontopsis bodei, Hyrachyus* cf. *modestus* (?middle Eocene), *Dilophodon* cf. *leotanus, Colodon* cf. *hancocki, ?Triplopus* cf. *implicatus,* and *?Triplopus* sp. The genera *Isectolophus, Epitriplopus,* and *?Forstercooperia* have not been recognized. Early Oligocene ceratomorphs of West Texas include *Metamynodon, Colodon stovalli* n. sp., *Hyracodon primus, Hyracodon petersoni,* and *Toxotherium hunteri. ?Toxotherium* sp., *?Trigonias* sp., and *?Caenopus* sp. are less certainly identified.

Epitriplopus medius is synonymized with *Epitriplopus uintensis* and at present we believe that it is confined to Uinta C and that there is no published evidence, beyond the list of Andersen and Picard (1972), that *Epitriplopus medius* occurs in the Lapoint. We also believe that *Mesamynodon medius* is confined to the Lapoint and should not be listed as part of the fauna of the Brennan Basin Member as was done by Andersen and Picard (1972). This species is an addition to the revision of the fauna of the Lapoint Member given by Emry (1981).

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